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UNIVERSITY OF ALBERTA

SYSTEMATICS OF NORTH AMERICAN *PETASITES* (ASTERACEAE: SENECIONEAE)

BY

© DONNA MARIE CHERNIAWKSY

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

IN

PLANT SYSTEMATICS

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL 1994

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Systematics of North American *Petasites*** (Asteraceae: Senecioneae) submitted by **Donna Marie Cherniawsky** in partial fulfillment of the requirements for the degree of **Master of Science** in **Plant Systematics**.

Dr. R.J. Bayer (supervisor)

Dr. D. H. Vitt

Dr. G.E. Ball

Dr. M.R.T. Dale

August 25, 1994

ABSTRACT

Petasites Mill. (Asteraceae: Senecioneae) is a genus of gynodioecious, perennial clonal herbs distributed across Canada, Alaska, and the northern contiguous United States. Due to the low variability in floral morphology and high diversity in leaf morphology, considerable taxonomic confusion surrounds the genus. This is reflected in the ambiguity of the various classification systems. As many as ten species and as few as two species have been recognized (*P. sagittatus* and *P. frigidus* with three varieties), in addition to one hybrid taxon. Morphological data were subjected to principal components and discriminant analyses to clarify the phenetic relationships among the various taxa of *Petasites*, particularly *P. frigidus* var. *frigidus, P. frigidus* var. *nivalis*, and the purported hybrid between these taxa which exhibits an intermediate morphology (the var. *frigidus* complex). Additionally, the status of *P. sagittatus* was investigated. Chromosome numbers were determined to further assess the relationships within *Petasites*. Genetic variation was assessed using starch gel electrophoresis and this also provided information with which to determine evolutionary relationships within the genus. Furthermore, the isozyme study contributed to the understanding of the population genetic structure of these clonal plants. Results from morphological and isozymic analyses were used to infer the mode of speciation and time since speciation events occurred in *Petasites*.

Evidence obtained from morphological and isozymic analyses indicates that North American *Petasites* is comprised of four closely related polymorphic entities. Morphological variation among different taxa of *Petasites* is continuous for most reproductive characters. Leaf characters proved to be the most taxonomically discriminating. The entities of the var. *frigidus* complex form a cohesive group while remaining somewhat distinct from the other taxa. Results obtained from the enzyme analysis indicate that the recognition of separate taxa in *Petasites* cannot be accomplished using information from isozymes. There are large interpopulational differences in allelic frequencies and although these differences are not specific to any particular taxon they suggest the occurrence of one large taxonomic group. The relatively high genetic identites among all taxa is indicative of conspecific populations and of a close relationship among taxa of *Petasites*. The genetic structure of populations of *Petasites* is comparable to other outcrossing clonal plant species; they exhibit a high genetic diversity which is partitioned mostly among populations. The similarity in isozymes, allozymes, and chromosome number, in conjunction with the close morphological associations is suggestive of a rapid and recent origin of *Petasites* in North America. It is postulated that the taxa indigenous to North America were derived from the circumpolar taxon, *P. frigidus* var. *frigidus*, through a process of adaptive radiation which began with the retreat of the first Wisconsinan glaciers.

In summary, the taxa of *Petasites* are not sufficiently differentiated, morphologically or isozymically, from the others to warrant the recognition of distinct species. The entities of the var. *frigidus* complex are united under one polymorphic taxon, *P. frigidus* var. *frigidus*. *Petasites sagittatus* is removed from the species rank to varietal status under *P. frigidus*. This systematic treatment of North American *Petasites* recognizes one highly polymorphic species, *P. frigidus*, with three varieties: var. *frigidus*, var. *sagittatus*, and var. *palmatus*. Additionally, the hybrid between *P. frigidus* var. *sagittatus* and var. *palmatus* is recogized as *P. frigidus* var. *X vitifolius*.

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CHAPTER ONE

INTRODUCTION

Plant systematics is the broad field of science concerned with the study of plant diversity. It is concerned with relationships among plant groups as well as their identification, description, classification, application of names, and their evolution. A systematic revision of a plant group is undertaken in order to resolve problems concerning the delimitation of taxa and the relationships among these taxa.

Petasites, a taxonomically difficult genus in the family Asteraceae, is in need of systematic revision. As an introduction to this revisionary study, a brief description of the Asteraceae and *Petasites* is provided. For a historical perspective, possible ancestral relationships of *Petasites* with other genera are reviewed. The general morphology and life history characteristics of *Petasites* are presented prior to a discussion of the taxonomic problems within this genus. The species concept and the focus of research in this study of *Petasites* are also addressed.

FAMILY ASTERACEAE

The Asteraceae is one of the largest and most successful families of the angiosperms (Cronquist 1988). The extensive diversification in life form, ecological tolerance, and adaptive strategies in the Asteraceae is reflected in its cosmopolitan distribution. The inflorescence, a capitulum or head, is the morphological feature uniting this family. Below the familial rank, however, it is the consistency of this feature which has generated considerable taxonomic confusion. This study focuses upon the taxonomic difficulties in one genus, *Petasites*, a member of the Tribe Senecioneae.

GENUS *PETASITES*

Petasites Mill. is a genus represented by diploid and triploid, rhizomatous perennial herbs commonly found in moist, disturbed habitats. The distribution of *Petasites* is circumpolar and it can be found in Britain, Europe, Asia, North Africa, (Stace 1989) and northern to central North America. All but one member of North American *Petasites* is indigenous to North America. The distribution of *P. frigidus* (L.) Fries var. *frigidus* extends to Europe and Asia. Within North America, *Petasites* is distributed across Canada, Alaska, and the northern contiguous United States.

Several hypotheses explaining the ancestral relationships of *Petasites* with other genera have been proposed. Stace (1989) suggested that *Petasites* belongs to the same lineage as other members of the Senecioneae, particularly *Endocellion*, *Homogyne*, and *Tussilago*, because these genera in the Senecioneae, as well as others, exhibit a basic chromosome number of $x = 30$ (Nordenstam 1977). *Homogyne* and *Tussilago* are most commonly associated with *Petasites* because they share the same somatic chromosome number ($2n = 60$) and a similar biochemistry (Robins 1977). *Tussilago*, in particular, is recognized as being closely related to *Petasites* by several authors (Cronquist 1955; Bogle 1961) including Linnaeus (1753). The circumpolar species of *Petasites* was originally described, by Linnaeus, as a species of *Tussilago*. The similarity between *Petasites* and *Tussilago* in morphology, biochemistry, and cytology provides the basis for a progenitor/derivative hypothesis in which *Petasites* is considered to be a derivative of *Tussilago*. The apparent disparity between breeding systems, monoecy in *Tussilago* and dioecy in *Petasites* is easily bridged. Dioecy may evolve from hermaphroditism via monoecy (Bawa 1980) therefore, such a proposal is plausible.

General Morphology and Life History

Petasites is depicted as a cohesive, relatively homogeneous group when represented by reproductive morphology. In terms of vegetative morphology, however, this genus emerges as a heterogeneous assemblage of various highly polymorphic entities.

Petasites is characterized by one to several primarily basal leaves with long petioles. Leaves arise alternately in the axils of bracts along the rhizome after, or with the emergence of flowering inflorescences. The diversity in leaf form is extensive in *Petasites*. Diversity is predominately attributed to variation in the degree of dissection, number of teeth, and shape of the leaf. Variation in leaf morphology encompasses an absence of lobes to the presence of distinct primary and secondary lobes with entire to denticulate margins, with shapes ranging from orbicular to sagittate. Further variation is exhibited by the numerous forms intermediate between these extremes.

Petasites is gynodioecious and the heads are arranged in racemose or corymbose clusters along the flowering stalk which arises from the rhizome. Cauline leaves along the flowering stalk are reduced to bracts which may possess an inflated lamina at the tip, typically similar in shape to the vegetative foliage.

Hermaphroditic heads consist of numerous perfect disc florets surrounded by a row of sterile, pistillate ray florets. The disc florets are functionally staminate and provide the only source of pollen. Therefore, hermaphroditic inflorescences are referred to as staminate in the remainder of the text.

Pistillate heads are comprised of numerous fertile, pistillate ray florets. The rays florets exhibit a reduction in length of the ray from the periphery to the center, where the corolla becomes filiform. In the center of the head are a few perfect, but sterile disc florets. Seed production occurs only in the pistillate inflorescences.

The flowering stalks commonly arise in early spring or early summer prior to, or with, the emergence of vegetative leaves. Pollination of the inflorescences is entomophilous and is

effected by a variety of insects including butterflies, bees, and beetles (Bogle 1961). Soon after anthesis the staminate inflorescences wither and die. After fertilization, however, the pistillate inflorescence elongates until the fruits have reached maturity. The fruit is an achene, equipped with white capillary bristles which function in wind dispersal.

Under moist conditions, seed germination occurs shortly after dispersal. Bogle (1961) reports that under very wet conditions, germination was initiated while seeds were still attached to the receptacle.

Taxonomic Problems

Although *Petasites* is clearly delimited from other genera in North America, the taxonomic limits within the genus are rather blurred. Since *Petasites* was first described, it has been surrounded by considerable taxonomic confusion.

North American species of *Petasites* has been recognized previously under two other generic names. Linnaeus (1753) described seven species of *Tussilago* in Species Plantarum. Four of these are now included in *Petasites*. Only one of these, *T. frigida*, is found in North America. In 1825, Cassini transferred several species of *Tussilago* to *Nardosmia*, including *T. frigida*. Most of the other North American taxa were named originally as species of *Tussilago*, then transferred to *Nardosmia*, and later to *Petasites*.

Numerous systematic treatments have been generated since Linnaeus' time. The manner of dealing with the continuous morphological variation in *Petasites* by most traditional taxonomists was to name new taxa on the basis of minor morphological differences. As many as ten species (Rydberg 1927), and as few as two species (Cronquist 1946) native to North America have been described. Although Hooker (1833) treated the various taxa at the specific rank, he recognized that these species were distinguished by only minute differences and noted that they all might be conspecific. However, it was after Herder's (1865) system that Cronquist (1946) ultimately modelled his systematic treatment. Cronquist (1946) recognized only two

species. One is the highly polymorphic species, *Petasites frigidus* with three varieties, and the other is the morphologically consistent *P. sagittatus*.

A major difficulty with the early classification systems is that they were based exclusively on differences in leaf morphology. Since the leaves exhibit a high degree of plasticity, however, the differences used to distinguish taxa are considered to be far from constant. The extent to which the environment can influence leaf morphology in *Petasites* is not known. This reduces the reliability of such classification systems considerably.

Current taxonomic problems still focus on the discordance among the systematic treatments in common use. The ambiguity of the relationships among the different plants is in need of resolution. The lack of clear demarcation among taxa is subsequently reflected in obscure keys which fail to reliably identify taxa. As a result, inadequate keys are in need of revision. In order to delimit the various taxa of *Petasites* and to determine the relationships among them, it is first necessary to define the species concept employed in this study.

Species Concept

The taxonomic species concept utilized in this study is considered to be the most practical and, therefore, the most workable for *Petasites*. It is best described by its author, Arthur Cronquist (1978): "*Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means.*"

The *smallest groups* criterion requires that groups cannot be further subdivided. The second criterion maintains that consistent features in an individual must conform to the range of variation within the group, and that the variation in this group must be discontinuous with the variation exhibited by other groups. All the individuals in question must clearly belong to one group and not the other (Cronquist 1978). The third criterion, being *persistently distinct*, specifies reproductive isolation (Cronquist 1978). There must be certainty that the offspring of a species will also belong to that species. Hybridization reduces the degree to which this

persistence criterion can be fulfilled. Lastly, the criterion of *ordinary means* must be considered. The aid of a hand lens or dissecting microscope typically satisfies this criterion for a field botanist. Although molecular techniques greatly enhance the understanding of relationships among different taxa, if there are no associated morphological markers, their value to the field botanist is minimal.

Focus of Research

All previous research in *Petasites* has been directed strictly toward the use of morphology. However, the current direction of research in *Petasites* is toward a multifaceted approach. Information obtained from studies in morphology, cytology, breeding system, isozymes, and phytogeography is used to investigate the phenetic and genetic relationships among populations and taxa of *Petasites*. From this revisionary study of *Petasites*, a classification system will be produced which reflects these relationships. Taxon descriptions, lists of nomenclatural and taxonomic synonyms, listings of representative specimens, distribution maps, ecological descriptions, and a key to facilitate the correct identification of specimens will also be included.

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CHAPTER TWO

SYSTEMTATIC INVESTIGATIONS OF NORTH AMERICAN *PETASITES*

INTRODUCTION

Petasites Mill. (Asteraceae: Senecioneae) is characterized as group of widespread, perennial, clonal herbs commonly living in disturbed habitats. These plants occur in small to large populations which tend to exhibit a patchy spatial distribution. The wide-ranging geographical distribution of North American *Petasites* extends from western to eastern Canada, Alaska, and the northern contiguous United States as far south as California. All North American taxa have sympatric ranges in northwestern North America.

Petasites possesses a suite of life history characteristics which has contributed to its successful colonization of various habitats and subsequent widespread distribution. Relevant to the distribution of *Petasites* is the utilization of both asexual and sexual modes of reproduction. Asexual reproduction is primarily responsible for the expansion of populations. The possession of an extensive, bracteate rhizome promotes the invasion and colonization of habitats through vegetative spreading. This oftem results in large clones that have been formed from a single vegetative fragment or seedling. The perennial habit of *Petasites* is responsible for the maintenance of populations, in addition to the accumulation of genetic variation, over long periods of time (Cheliak and Dancik 1982). And certainly, the capacity for long distance seed dispersal is a factor which has facilitated *Petasites* in achieving of such an extensive distribution in North America. Although dioecy may inhibit sexual reproduction to some degree, this is considered minimal in *Petasites* because all populations observed in the field were comprised of both staminate and pistillate plants.

TAXONOMIC PROBLEMS

Petasites is a polymorphic genus currently represented in North America by five ill-defined native taxa and two introduced species (*P. japonicus* Maxim., and *P. hybridus* (L.) Gaertn., Mey. & Sherb.). *Petasites* has been taxonomically perplexing from the time it was originally described to the present day. A major difficulty has been the exclusive use of minor differences in leaf morphology for species definition and recognition. This has proven to be problematic because the leaves exhibit a high degree of plasticity, therefore, the differences used to distinguish taxa are far from constant. The relationships between leaf form and taxonomic identity have not been unanimously defined. This is reflected in the ambiguity of the classification systems in current use. See Table 2-1.

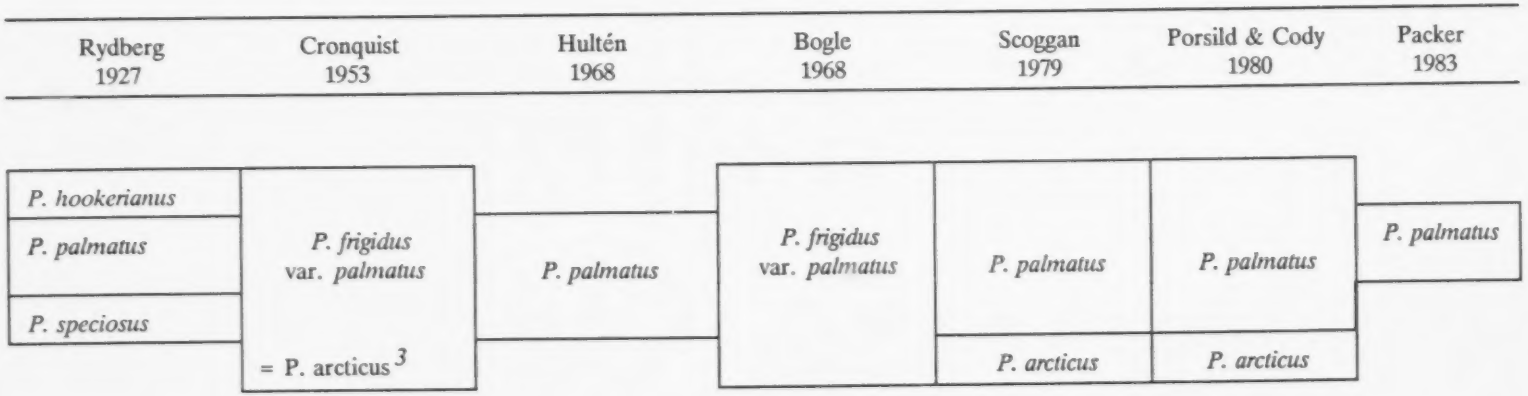
The circumscription of North American *Petasites* varies substantially. On one extreme, Rydberg (1927) recognized ten species, whereas Cronquist (1953) and Bogle (1968), on the other extreme, recognized only two (Table 2-1). Although intergradation, and therefore hybridization, of the different taxa was evident, and although most authors acknowledged it, few accounted for it in their systematic treatments. Only two of the classification systems have attempted to accomodate the morphological variation observed in this polymorphic genus.

Hultén (1950) was the first to include hybridization in his systematic treatment. Bogle (1968) agreed with the circumscriptions of Hultén for the most part, although he ranked the taxa at the varietal level, as Cronquist (1946) had done formerly. Bogle also made several significant contributions to the understanding of relationships within the genus, particularly the discovery of the hybrid origin of *Petasites vitifolius* (= *P. X vififolius sensu* Bogle). However, later treatments continued to retain this taxon at the specific rank.

The current taxonomic problem addressed in this study focuses on the discordance among the various systematic treatments (Table 2-1). The ambiguity of the relationships among the different taxa is in need of resolution, particularly *Petasites frigidus* var. *frigidus*, *P. frigidus* var. *nivalis*, and the proposed hybrid between these taxa (Hultén 1950) which exhibits an

Table 2-1. Comparative systematic treatments of North American taxa of *Petasites* The squares denote the circumscription of the various taxa. Empty squares indicate that the author has not included that particular taxon in his treatment.

Rydberg 1927	Cronquist 1953	Hultén 1968	Bogle 1968	Scoggan 1979	Porsild & Cody 1980	Packer 1983
P. sagittatus = *P. dentatus*	*P. sagittatus*	*P. sagittatus*	*P. sagittatus*	*P. sagittatus*	*P. sagittatus*	*P. sagittatus*
		* *P. frigidus X P. sagittatus*	* *P. f.* var. *frigidus X P. sagittatus*			
P. alaskanus [1]	*P. frigidus* var. *frigidus* = *P. warrenii*	*P. frigidus*	*P. frigidus* var. *frigidus*	*P. frigidus*		
P. gracilis [2]						
P. frigidus					*P. frigidus*	*P. frigidus*
		** *P. frigidus X P. hyperboreus* = *P. f.* var. *hyperboreoides* = *1, 2, 3*	** *P. f.* var. *frigidus X P. f.* var. *nivalis*	*P. vitifolius*		
P. nivalis	*P. frigidus* var. *nivalis*		*P. frigidus* var. *nivalis*			*P. nivalis*
P. hyperboreus		*P. hyperboreus*			*P. hyperboreus*	
P. vitifolius			*P. X vitifolius* = *P. f.* var. *palmatus X P. sagittatus* = *P. warennii*		*P. vitifolius* = *P. f.* var. *palmatus X P. sagittatus*	*P.vitifolius* = *P. f.* var. *palmatus X P. sagittatus*



* denotes the hybridization between *P. frigidus* and *P. sagittatus* as proposed by Hulten and supported by Bogle.

** denotes the hybridization between *P. frigidus* and *P. hyperboreus* as proposed by Hulten. Hulten designated this hybrid as *P. frigidus* var. *hyperboreoides* and included *P. alaskanus, P. gracilis,* and *P. arcticus* as additional products of such hybridization events. This proposal has been supported by Bogle, although he preferred to recognize *P. frigidus* as the typical variety of this species and *P. hyperboreus* as *P. frigidus* var. *nivalis*

intermediate leaf morphology. Consequently, the obscure boundaries among the taxa of *Petasites* is reflected in inadequate keys to reliably identify taxa. A set of morphological characters that can reliably discriminate among the various taxa is required.

TAXA OF NORTH AMERICAN *PETASITES*

The working classification of the taxa of *Petasites* follows the systematic treatment of Bogle (1968). See Table 2-1. Six groups are recognized. *Petasites frigidus* var. *frigidus*, *P. frigidus* var. *nivalis*, and the forms intermediate in morphology between these taxa are collectively referred to as the var. *frigidus* complex. Individually, these varieties are referred to *sensu stricto* and the intermediates denoted simply as the intermediates. *Petasites frigidus* var. *palmatus*, *P. sagittatus*, and *P. X vitifolius* are recognized *sensu* Bogle. For the purpose of brevity, the varieties may be designated simply as e.g. var. *palmatus*. Figures 2-1 to 2-16 provide comparative illustrations of the six groups. A brief description of the general leaf morphology and distribution of each taxon is provided here.

Petasites frigidus (L.) Fries var. *frigidus* is characterized by sagittate, deltoid, to cordate leaf blades which are regularly or irregularly dentate, or very shallowly or deeply, equally or unequally lobed. Figures 2-1 to 2-3 illustrate the variable leaf morphology in this taxon. Plants of this taxon generally are of a small stature with relatively delicate petioles, although leaf lengths of almost 21 cm have been observed. *Petasites frigidus* var. *frigidus* commonly occurs along moist alpine and subalpine slopes, although it may also be found growing along streams, in marshes, along edges of forests, and gravelly roadsides. The geographical range of this taxon includes North America and Eurasia. Compared to the other taxa of *Petasites* in North America, var. *frigidus* exhibits the most restricted range. It is common in Alaska, the Yukon, the Northwest Territories and several Arctic islands. Its distribution reaches more southern limits in high mountain areas of British Columbia and Alberta.

Figure 2-1. Specimen of *Petasites frigidus* var. *frigidus* (*sens. strict.*) exhibiting typical leaf morphology. *A.R. Batten 226* (ALA-52583).

Figure 2-2. Specimen of *Petasites frigidus* var. *frigidus* (*sens. strict.*) exhibiting typical leaf morphology. *S.G. Aiken and K.I. McLachlan 87-144* (CAN-530972).

Figure 2-3. Specimen of *Petasites frigidus* var. *frigidus* (*sens. strict.*) exhibiting typical leaf morphology. *R.T. Porsild 1384* (CAN-318264). Bar = 4 cm.

Figure 2-4. Specimen of *Petasites frigidus* var. *nivalis* exhibiting highly dissected leaf morphology. *W.C. McCalla 9307* (ALTA-67297). Bar = 4 cm.

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Petasites frigidus var. *nivalis* (Greene) Cronq. exhibits the highest degree of leaf dissection of all North Amercian taxa. The most extreme forms are five-parted and shallowly to deeply lobed, many lobes have at least two lateral triangular teeth which frequently overlap, and sinuses are oblong and closed. Figures 2-4 and 2-5 represent this extreme leaf form. Figure 2-6 represents a leaf form which exhibits a lesser degree of dissection. The adaxial surface of leaves is glabrous to tomentose and the abaxial surface is glabrous to woolly. *Petasites frigidus* var. *nivalis* inhabits moist alpine to subalpine slopes, although it is frequently found at high altitudes, but also occurs at lower altitudes of approximately 1050 m (Bogle 1961). Both the habitat and geographic range of var. *nivalis* is considered to be concurrent with much of the range of var. *frigidus* in Alaska, the Yukon and the southwest Mackenzie District. However, it is absent from arctic Canada and east Keewatin District. *Petasites frigidus* var. *nivalis* extends southward to British Columbia, Alberta, and Washington.

Specimens in Figures 2-7 to 2-9 represent leaf forms intermediate between *Petasites frigidus* var. *frigidus* and var. *nivalis*. Hultén (1950) considered these leaf forms to be hybrids between var. *frigidus* and var. *nivalis*. He proposed the name *Petasites frigidus* var. *hyperboreoides* to accomodate these leaf forms (Hultén 1937). Figures 2-10 and 2-11 illustrate specimens with leaves characteristic of both var. *frigidus* and var. *nivalis*.

Petasites frigidus var. *palmatus* (Ait.) Cronq. is characterized by orbicular to reniform leaf blades with deeply divided foliage of five to nine entire or dentate lobes divided more than half way to the leaf base. Some western specimens possess as many as 11 lobes, most of which are divided only about half way to the base. Leaves are completely glabrous to pillose on the adaxial surface and glabrous to tomentose on the abaxial surface. Figure 2-12 illustrates the most typical leaf shape of this variety. Like the other taxa the size of this taxon is highly variable. Small delicate forms only a few cm in width and length have been observed, many from forested regions, whereas Bogle (1961) described more robust specimens with leaves up to 50 cm wide and 40 cm long in Washington and Oregon. *Petasites frigidus* var. *palmatus*

Figure 2-5. Specimen of *Petasites frigidus* var. *nivalis* exhibiting highly dissected leaf morphology. *E.D. Greene s.n.* (NDG-062358).

Figure 2-6. Specimen of *Petasites frigidus* var. *nivalis* exhibiting less highly dissected leaf morphology. *D.J. Cooper 1080* (ALA-98624). Bar = 4 cm.

Figure 2-7. Specimen of plant exhibiting leaf morphology intermediate between *Petasites frigidus* var. *frigidus* (*sens. strict.*) and *P. frigidus* var. *nivalis*. *F.W. True and D.W. Prentis, Jr. 37* (US-241413). Bar = 4 cm.

Figure 2-8. Specimen of plant exhibiting leaf morphology intermediate between *Petasites frigidus* var. *frigidus* (*sens. strict.*) and *P. frigidus* var. *nivalis*, arrow indicates leaf form that is similar to *P. tatewakianus*. *C. Schweger 178* (ALA-3422).

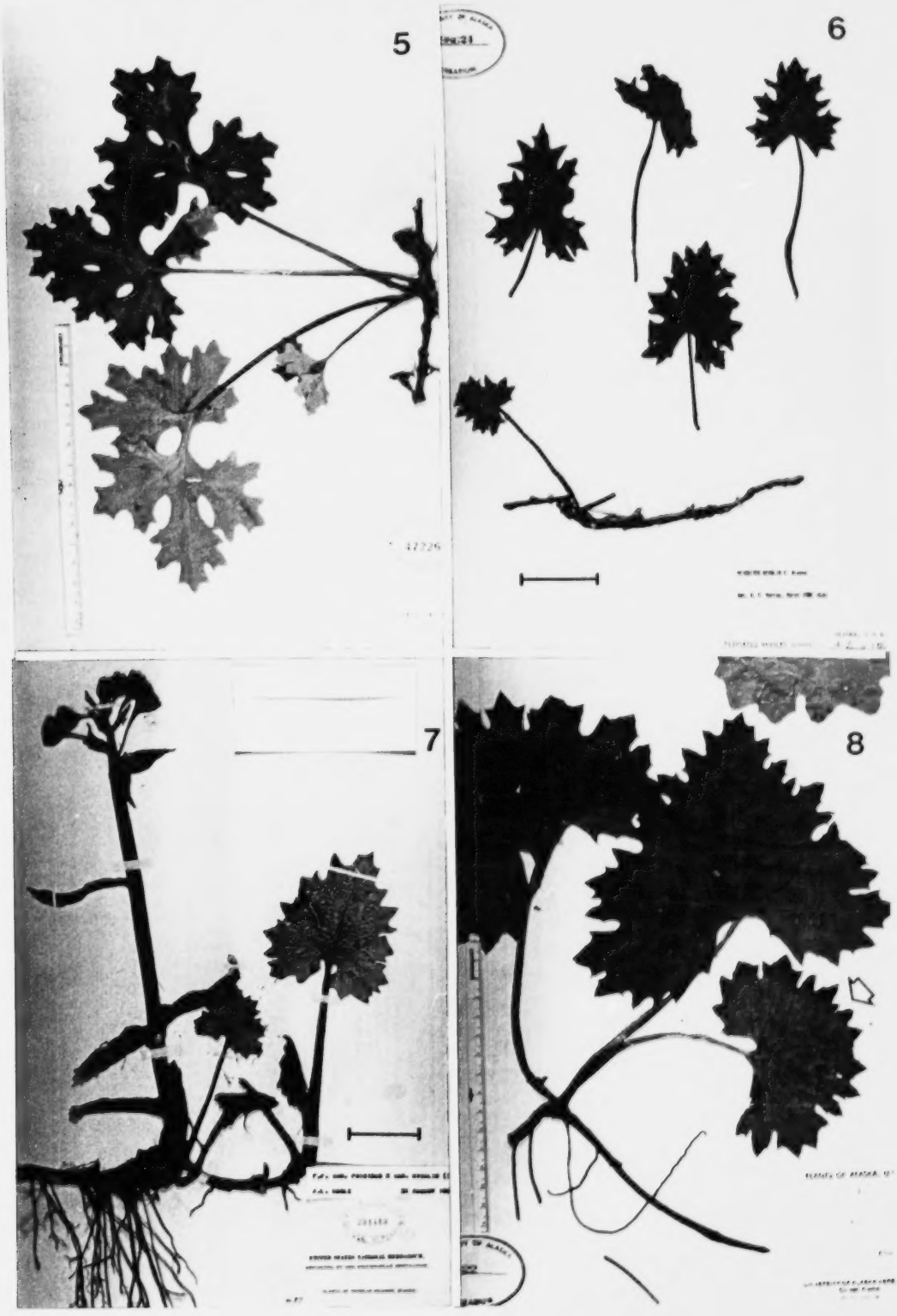
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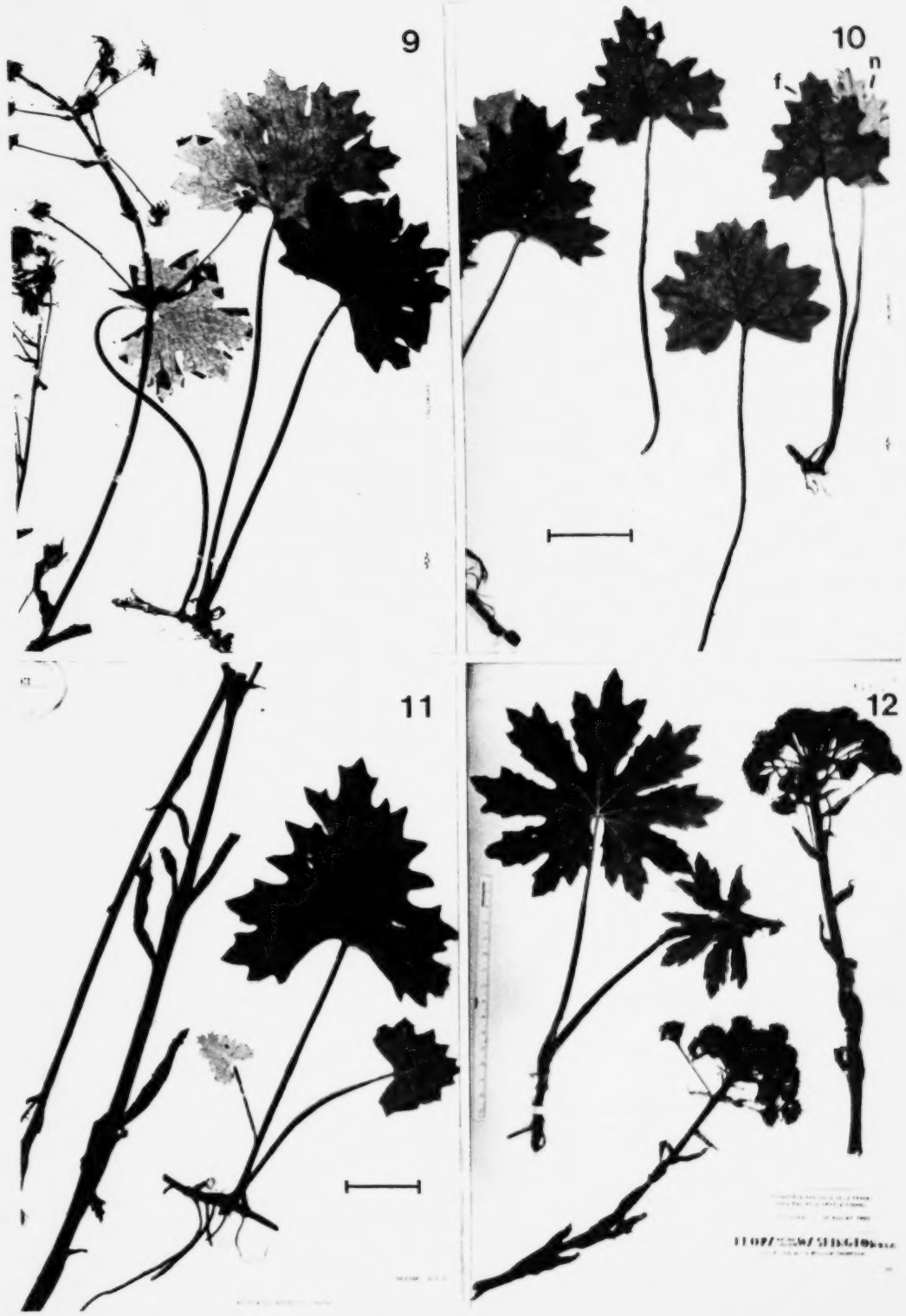
Figure 2-9. Specimen exhibiting a leaf morphology similar to *Petasites frigidus* var. *palmatus* and *P. frigidus* var. *frigidus*. Possibly a hybrid between these two varieties. *R.H. Day and A.A. Hoover 79-85* (ALA V95354). Bar = 4 cm.

Figure 2-10. Specimen possessing leaves characteristic of both *Petasites frigidus* var. *frigidus* (*sens. strict.*) and *P. frigidus* var. *nivalis*, f = *P. frigidus* var. *frigidus* (*sens. strict.*), n = *P. frigidus* var. *nivalis*. *R. Brockman 25* (ALA-28549). Bar = 4 cm.

Figure 2-11. Specimen possessing leaves characteristic of both *Petasites frigidus* var. *frigidus* (*sens. strict.*) and *P. frigidus* var. *nivalis*. *A. Batten 76-134* (ALA-78703). Bar = 4 cm.

Figure 2-12. Specimen of *Petasites frigidus* var. *palmatus* exhibiting leaf morphology typical of this variety. *W.C. McCalla 11308* (ALTA-67285).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inhabits moist soils of disturbed sites such as road cuts, embankments, stream banks, and roadsides. This plant is also commonly found in moist woods, in addition to extremely dry, sandy or gravelly roadsides. *Petasites frigidus* var. *palmatus* is widely distributed across Canada and the northern United States. It extends from northwest Yukon to the west Mackenzie District and across all provinces of Canada. Its range extends southward to Maine, Massachusettes, and New York and continues westward to Michigan, Wisconsin, Minnesota, Washington, Oregon and as far south as Monterey County in California (Bogle 1961).

Hultén (1950) and Bogle (1868) have acknowledged the presence of *Petasites frigidus* var. *palmatus* in extreme eastern Siberia. This is based on the palmately leaved specimen *P. tatewakianus* described by Kitamura (1940) from Sakhalin Island, USSR. Kitamura (1940) differentiated this species from var. *palmatus* on the basis of degree of leaf dissection, ray length, and achene length. It possesses a leaf form similar to var. *palmatus* although the lobes are only dissected about one third to the center. Ray length is within the range of all North American *Petasites*, although the upper range of achene length in *P. tatewakianus* is reached only in var. *palmatus*. At this time, however, it is questionable whether or not this Asiatic species is synonymous with North American var. *palmatus*. The status of *P. tatewakianus* is discussed in more detail in Chapter Four under Phytogeography.

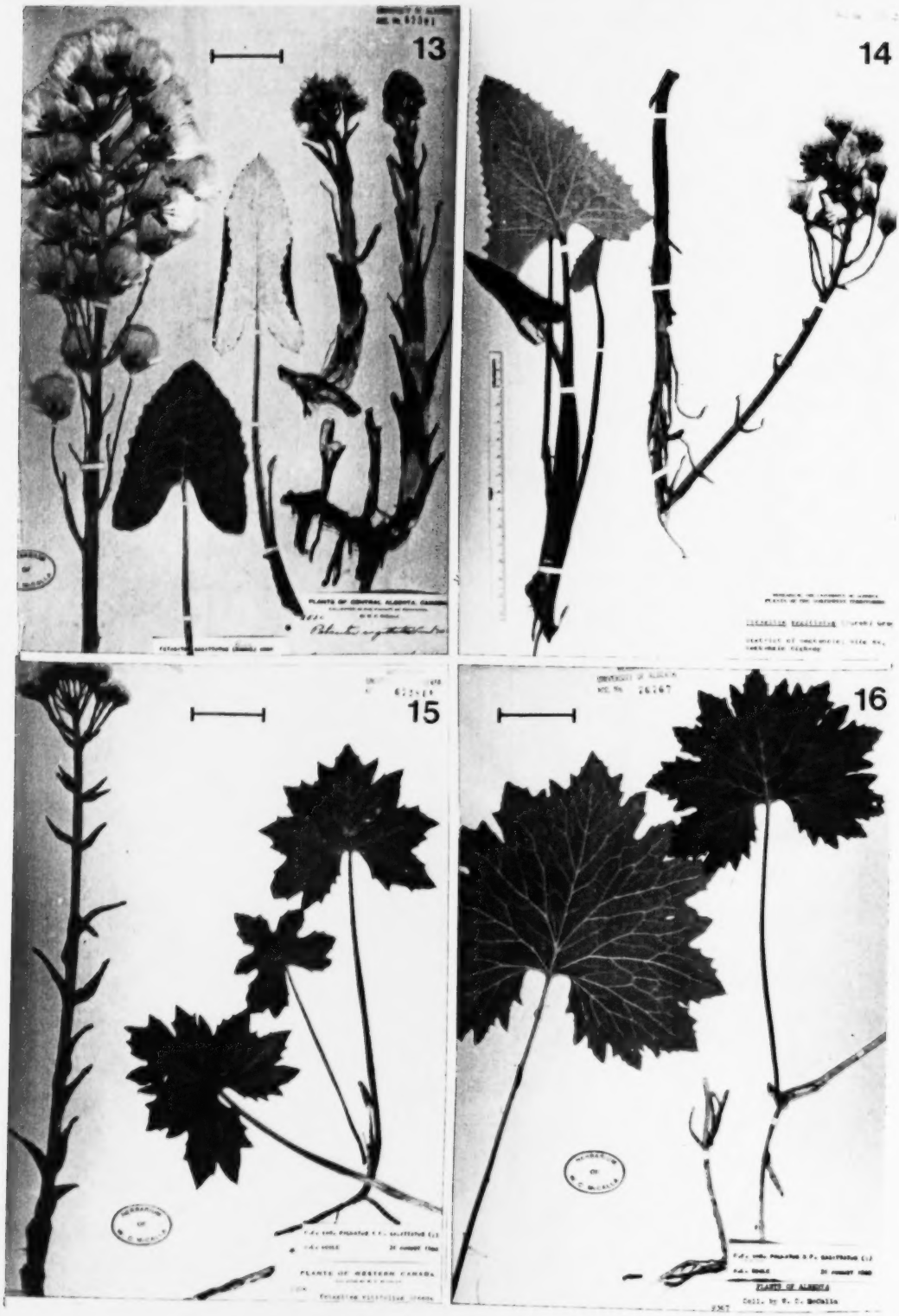
Petasites sagittatus (Banks ex Pursh) Gray is characterized by sagittate and deltoid to cordate leaf blades. Leaves are entire to dentate varying from wavy to conspicuously dentate. The adaxial surface of leaves is glabrous to densely tomentose, and the abaxial surface is extremely woolly. Figure 2-13 illustrates a sagittate leaf blade, whereas Figure 2-14 portrays a leaf blade that is more deltoid. This plant thrives under wet conditions in bogs, fens, and marshes. It is found growing in shallow standing water with rhizomes buried in mud and commonly occurs in disturbed sites such as clearcuts and roadsides. Additionally, *P. sagittatus* is often found growing in association with var. *palmatus* and *P. X vitifolius*. It has been observed growing at an elevation as high as 3,000 m (Bogle 1961). The geographic range of *Petasites*

Figure 2-13. Specimen of *Petasites sagittatus*. *W.C. McCalla 2530* (ALTA-67301). Bar = 4 cm.

Figure 2-14. Specimen of *Petasites sagittatus*. *S.S. Talbot 2186* (ALTA-49620).

Figure 2-15. Specimen of *Petasites X vitifolius*. *W.C. McCalla 3704* (ALTA-6728). Bar = 4 cm.

Figure 2-16. Specimen of *Petasites X vitifolius*. *W.C. McCalla 9367* (ALTA-76767). Bar = 4 cm.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sagittatus is similar to that of var. *palmatus* although it does not extend into California. Its distribution includes Alaska, the Yukon, the Mackenzie District to Hudson's Bay, Quebec, New Brunswick, Ontario, Manitoba, Saskatchewan, Alberta, and British Columbia. It extends southward to northeast Washington, northern Idaho, Montana, Wyoming, Colorado, North Dakota, South Dakota, northern Minnesota, northern Wisconsin, and northern Michigan.

The hybrid *Petasites X vitifolius* Greene exhibits a morphology intermediate to its parental species, *P. frigidus* var. *palmatus* and *P. sagittatus*. It is characterized by reniform to deltoid or cordate leaf blades which are usually widest at the base with convex-curved edges. There are 4-14 shallow, entire to dentate triangular primary lobes, and as many as 11 secondary lobes. The adaxial surface of leaves is glabrous to tomentose and the abaxial surface is glabrous to woolly. See Figures 2-15 and 2-16. Bogle (1961) reports specimens with leaves 47 cm wide and 43 cm long. Additionally, many juvenile forms closely resemble *P. frigidus* var. *frigidus* (Bogle 1961). *Petasites X vitifolius* is commonly found in wet conditions preferred by *P. sagittatus* but also lives in drier regions in association with var. *palmatus* and *P. sagittatus*. The geographical range of this hybrid is within the confines of distribution of var. *palmatus* and *Petasites sagittatus*, but is less extensive than the range of either parent. Its distribution includes southeastern Yukon, southwest Mackenzie District, British Columbia, the prairie provinces of Canada, Ontario, central Quebec, Labrador, and south to northern Michigan, northern Minnesota, and Washington State.

PREVIOUS RESEARCH

The most recent systematic work on *Petasites* was by Bogle (1961). Except for chromosome counts, no other research had been performed on the North American taxa.

Bogle investigated *Petasites warrenii* St. John, a supposed endemic of the state of Washington. Through a series of crossing studies, Bogle elucidated the relationship of this species with the other taxa of *Petasites*. From his research, Bogle (1961) concluded that

Petasites warrenii St. John, *P. vitifolius* Greene, and *P. trigonophylla* Greene were all members of a large, diverse group originating in hybridization between *P. sagittatus* (Banks ex. Pursh) Gray and *P. frigidus* var. *palmatus* (Ait.) Cronq. Bogle (1961) understood these taxa to represent polymorphic variants consisting of F_1, F_2, and F_3 hybrids, in addition to those obtained from backcrossing to the parental species. Much of the resultant variation was comparable to that which was previously relegated to *Petasites vitifolius*. High fertility in the F_1 hybrids and some fertility in the more complex hybrid generations has been demonstrated by Bogle (1968). In 1968, Bogle proposed the hybrid designation, *Petasites X vitifolius* Greene (pro sp.) to include *P. warrenii, P. trigonophylla*, and *P. vitifolius*.

Bogle's observations of some *Petasites* populations comprised entirely of pistillate plants initially suggested the occurrence of agamospermy. However, he found no evidence for this phenomenon in *Petasites*.

CURRENT RESEARCH IN SYSTEMATICS

Systematic and phylogenetic inferences made by classical systematists were founded largely on morphological attributes of plant groups. The assumption was that morphological variation reflected genetic variation. However, many morphological traits are controlled by only one or two genes (Cutter 1971; Gottlieb 1984). Further reducing the reliablility of morphological data alone as an indicator of genetic relationships is the influence of environmental factors on morphology.

Modern methods continue to use morphologically-based evidence to determine phenetic relationships in plant groups. However, morphological features are further analysed using statistical techniques. Multivariate morphometric analyses, including principal components analyses and discriminant analyses, provide an assessment of morphological relationships of various taxa. They help ascertain which characters provide the greatest contribution to the overall variation in the group. Additionally, they aid in the determination of characters which

provide the best discrimination among taxa with limited *a priori* weighting of the characters. Chromosome number determinations continue to be useful measures of genetic similarity. They provide data on ploidy levels and may help elucidate the origins of taxa.

Systematists now rely heavily on molecular evidence in conjunction with morphological and cytological data as indicators of genetic differentiation. Enzyme electrophoresis has become a powerful tool in the genetic analyses between and among populations and taxa. There are a number of advantages for the use of electrophoretic evidence over morphological and secondary chemistry data.

Firstly, there is no *a priori* character weighting in electrophoretic data as is the case when one chooses morphological characters thought to be of taxonomic value. All loci are given equal weight (Crawford 1983). Secondly, since isozymes (polypeptides coded by more than one gene locus) are proteins, they are products of genes. As opposed to many morphological differences which are under the influence of environmental conditions, differences among isozymes reflect differences in the DNA sequence. Thirdly, because allozymes (polypeptides coded by different alleles at a single gene locus) show codominant inheritance and segregate as single Mendelian factors, band interpretation is relatively straightforward (Crawford 1990).

The range of applications of electrophoretic evidence in plant systematics is broad. Electrophoretic evidence permits the assessment of genetic diversity within and among populations and taxa. Subsequently, genetic divergence estimates can be effectively used to clarify relationships among taxonomically difficult taxa. Moreover, the amount and distribution of genetic diversity has important evolutionary implications for the discovery and understanding of origins of taxa and modes of speciation. Genetic diversity statistics can also provide information on breeding systems and the effects they have on genetic variability. Furthermore, electrophoretic evidence provides the tools with which to study the genetic structure of

populations. This is particularly important in this study of *Petasites*, as it provides an additional contribution to the limited number of studies available on clonal plant species.

RESEARCH OBJECTIVES

The necessity for a classification system and reliable key to accomodate the morphological variation in *Petasites* is addressed. To enable the provision of a workable key, a set of morphological characters which delimits precisely the various taxa must first be selected. The selection of characters is determined in this chapter. A key is provided in Chapter 3. Only with the elucidation of the evolutionary relationships among the different taxa of *Petasites* is it be possible to provide a classification system which best reflects these evolutionary relationships. Furthermore, this study attempts to obtain an understanding of the genetic structure of populations of *Petasites* and the dynamics operating within them. Therefore, the primary objectives of this research are:

1) to delimit the taxa and the various phenetic relationships within the North American taxa of *Petasites* using morphometric analyses;

2) to determine the evolutionary relationships within *Petasites* through the use of starch gel electrophoresis of enzymes, in addition to comparisons of chromosome numbers;

3) to obtain an understanding of the population structure in *Petasites*, from the interpretation of genetic diversity results obtained from the enzyme analysis, and to relate this to the life history characteristics of this genus, and;

4) to provide a classification of *Petasites* which better expresses evolutionary relationships among the taxa, based on the interpretation of results from the above-mentioned studies, and which conforms to the species concept utilized in this study.

MATERIALS AND METHODS

FIELD STUDIES AND COLLECTIONS

Field work was carried out at three different time intervals: the spring of 1991, summer of 1992, and the summer of 1993. Plants used in the morphological study and part of the cytological study were collected in the spring of 1991 from 51 populations in Alberta, British Columbia, the Yukon Territory, and Alaska (vouchers are deposited at ALTA). This field season was scheduled during the spring in an attempt to observe sex ratios in populations of *Petasites* while individuals were still in flower. All North American taxa of *Petasites* were sampled.

Plants used in the electrophoretic study and part of the cytological study were collected from 47 populations in the summer of 1992 from Alberta, British Columbia, the Yukon Territory, the Northwest Territories, and Alaska (Table 2-2). Since the material obtained during this period was for electrophoretic and cytological purpose, it was not essential that the plants were in flower. Plants from six populations of *Petasites X vitifolius* were collected in the summer of 1993 (Table 2-2). These specimens were used to complete the electrophoretic study.

Depending on the size of the population, 20 to 30 individuals per population were randomly sampled. Due to the rhizomatous habit of *Petasites*, plants were collected a few meters apart to avoid sampling from the same vegetative clone.

Rhizomes were collected during the first two field seasons, packed in moist Sphagnum, and stored in refrigeration. Seeds were collected when available and stored in paper bags. Only leaves of *Petasites X vitifolius* were collected in 1993. Several plants from each population were pressed as vouchers. Additionally, information on habitat, sex ratios, and community associations was recorded for each population.

Table 2-2. Locality data for 47 population samples of *Petasites* used in the isozyme study. Population designation consists of province/state, year, and collection number. Vouchers are deposited at ALTA.

TAXON	LOCALITY	POPULATION DESIGNATION
P. frigidus var. *frigidus*	ALASKA, Eagle Quad.: Black spruce forest on W. side of Taylor Hwy., 2.3 km S. of Milepost 136. 64° 30' N, 141° 15' W.	AK-92026
	ALASKA, Eagle Quad.: West-facing slope of American Summit at Mile 142 of Taylor Hwy., alpine tundra. 64°38' N, 141°20' W.	AK-92027
	ALASKA, Eagle Quad.: Roadside N. of Taylor Hwy., 7.8 km E. of Lost Chicken Hill in *Picea glauca, Populus tremuloides, Salix* forest. 64°05' N, 141°50' W.	AK-92028
	ALASKA, Tanacross Quad.: "Chicken Burn", E. side of Taylor Hwy., at Km 82.2, 1.3 km N. of Taylor Creek Bridge. 63°25' N, 142°20" W.	AK-92029
	ALASKA, Circle Quad.: Eagle Summit, rocky alpine tundra, alt. 1250 m. 65°32'N, 145°30'W.	AK-92031
	ALASKA, Philip Smith Mts. Quad.: Galbraith Lake, tundra, 15 m off road. 68°25' N, 149°25' W.	AK-92032
	ALASKA, Sagavanirktok Quad.: South-facing slope beneath solifluction lobes at extreme N. end of Chandalar Shelf approx. 2 km S. of Atigun Pass at headwaters of N. fork of Chandalar R. 69°06' N, 149°32' W.	AK-92033
	ALASKA, Mt. Hayes Quad.: Alpine ridge-top below Rainbow Ridge, gravelly willow thicket, alt. 1100 m. 63°15' N, 145°40' W.	AK-92034
	Northwest Territories, Arctic Red River Quad.: S.E. side of Dempster Hwy., 30 km N. of Yukon/N.W.T. border, alt. 845 m. 67°10'N, 136°' W.	NW-92021
	Northwest Territories, Arctic Red R. Quad.: Roadside of Dempster Hwy., 42.9 km N. of the Yukon/N.W.T. border. 67°12' N, 135°40' W.	NW-92022
	YUKON, Pelly River Quad.: Km 49.5 of North Canol Road. 62°11.5' N, 131°48' W.	YT-92036
	YUKON, Pelly R. Quad.: S. side of Canol Road E. of Macmillan Pass, alt. 1240 m. 63°15'N, 130°41'W.	YT-92037

TAXON	LOCALITY	POPULATION DESIGNATION
	YUKON, Pelly R. Quad.: Keno Hill, 200 m S. of signpost, wet clay and mossy areas, alt. 1890 m. 63°55' N, 135°18' W.	YT-920161
	YUKON, Pelly R. Quad.: Keno Hill, 1.5 km S. of signpost. 63°56' N, 135°18' W.	YT-920162
	YUKON, Pelly R. Quad.: South-facing slope of Keno Hill, 1 km E. of signpost, rocky alpine tundra, alt. 1720 m. 63°55' N, 135°17' W.	YT-92017
	YUKON, Fort Selkirk Quad.: Edge of campground opposite Ethel Lake in wet *Sphagnum* in *Salix/Picea mariana* forest. 63°30' N, 136°20' W.	YT-92015
	YUKON, Klondike Quad.: West-facing slope across from Tombstone Mt. sign, along Dempster Hwy., 2.5 km N. of Tombstone Mt. Campground, alt. 1481 m. 64°23' N, 138°21' W.	YT-92018
	YUKON, Klondike Quad.: Hillside NW. of Dempster Hwy. at Km 130.4 in dense *Betula glandulosa* and *Salix* shrubs with *Picea glauca*, alt. 1180 m. 65°05' N, 138°21' W.	YT-92019
	YUKON, Klondike Quad.: Km 9.6 on Sixty Mile Rd., off Klondike Loop, roadside at edge of *Picea mariana, Salix, Sphagnum* bog, alt. 1070 m. 64°03' N, 140°43' W.	YT-92025
	YUKON, Porcupine River Quad.: Richardson Mts., roadside E. of Dempster Hwy. at Km 454, arctic tundra, alt. 1080 m. 66°36' N, 136°19' W.	YT-92020
	YUKON, Porcupine R. Quad.: E. of Dempster Hwy., 1 km S. of Arctic Circle sign, gravelly roadside. 63°33.5' N, 136°20' W.	YT-92023
	YUKON, Whitehorse-Teslin Quad.: West-facing slope at Km 71.7 of Klondike Loop, alt. 1425 m. 61°19' N, 135°37' W.	YT-92024
P. frigidus var. *palmatus*	ALBERTA, Clearing in *Populus tremuloides/ Picea* forest at edge of roadside, 2.5 km N. of Hwy. 16X, 23 km W. of Edmonton. 55°33' N, 113°28' W.	AB-92001
	ALBERTA, U. of A. Ecological Reserve, N. side of 116 St. and Sask. Drive, Edmonton, *Populus tremuloides/Picea glauca* forest. 55°33' N, 113°28' W.	AB-92002

TAXON	LOCALITY	POPULATION DESIGNATION
	ALBERTA, U. of A. Ecological Reserve, Edmonton, 10 m S. of river on north-facing slope. 55°33' N, 113°28' W.	AB-92003
	ALBERTA, U. of A. Ecological Reserve, near path 100 m below 111 St. and Sask. Drive, Edmonton. 55°33' N, 113°28' W.	AB-92004
	ALBERTA, 15 km W. of Buzby on Hwy. 651, grassy field, associated with *P. sagittatus*. 54° N, 114°05' W.	AB-92008
	British Columbia, Prince George-Dawson Creek Quad.: Roadside ditch, at edge of *Populus tremuloides/Salix* forest, 12.5 km S. of Dawson Creek, on Hwy. 49. 55°44' N, 120°08' W.	BC-92010
	British Columbia, Hudson Hope Quad.: Turnoff to Trutch Mt. Historical Site, 83.5 km SE of Prophet River, roadside at edge of *Picea glauca* and *Pinus contorta* forest. 57°27' N, 122°53' W.	BC-92012
	Northwest Territories, Arctic Red R. Quad.: S.E. side of Dempster Hwy., 30 km N. of Yukon/N.W.T. border. 67°10'N, 136°' W.	NW-92021
	Northwest Territories, Arctic Red R. Quad.: Roadside of Dempster Hwy, 42.9 km N. of the Yukon/N.W.T. border. 67°12' N, 135°40' W.	NW-92022
	YUKON, Wolf Lake-Watson Lake Quad.: Turnout on N. side of Alaska Hwy., 3.4 km W. of Little Rancheria Creek Bridge, at edge of *Pinus contorta* and *Salix* forest. 60°10.5' N, 129°47' W.	YT-92014
	YUKON, Porcupine R. Quad.: E. of Dempster Hwy., 1 km S. of Arctic Circle sign. 66°33.5' N, 136°20' W.	YT-92023
P. sagittatus	ALBERTA, Kinsella Ranch, Section 28, E. of *Carex/Populus tremuloides/Salix* stand, 1 km S. of salt lake. 53° N, 111°32' W.	AB-92005
	ALBERTA, Alongside road to bird sanctuary on Secondary Hwy. 834 near Tofield, 5.5 km N. of Sears Elementary School, in mud in tight association with grasses. 53°22' N, 112°40' W.	AB-92006
	ALBERTA, Field, 15 km W. of Buzby on Hwy. 651, associated with *P. frigidus* var. *palmatus*. 54° N, 114°05' W.	AB-92007

TAXON	LOCALITY	POPULATION DESIGNATION
	ALBERTA, Large field, 11.4 km W. of 79th St. and Whitemud Drive, 2.8 km S. of Range Road 270, Edmonton. 55°33' N, 113°28' W.	AB-92009
	ALASKA, Tanacross Quad.: 4 km W. of Tetlin Junction on N. side of Alaska Hwy, at Milepost 1306, swampy region at boundary of *Picea* burn. 63°20' N, 143° W.	AK-92030
	British Columbia, Hudson Hope Quad.: 4 km N. of Sikanni on Alaska Hwy., ditch at edge of *Populus tremuloides* forest. 57°13' N, 121°42' W.	BC-92011
	British Columbia, Liard River Quad.: Roadside at edge of *P. tremuloides/Salix* forest S. of Alaska Hwy., 3.8 km E. of Toad River Bridge. 58°50' N, 125° W.	BC-92013
	YUKON, St. Elias Quad.: Pine Lake Campground outside of Haines Junction. 60°49' N, 137°27' W.	AK-92035
P. X vitifolius	ALBERTA, 13.1 km W. of Buzby on Hwy. 651, roadside ditch at edge of *Populus balsamifera* and *Salix* forest beside George Lake, associated with *P. frigidus* var. *palmatus*. 54° N, 113°59' W.	AB-93038
	ALBERTA, 1.6 km E. of Sec. Hwy. 777, along roadside leading to George Lake Field Station, approx. 50 m from hwy, sandy soil at edge of *Populus tremuloides* and *Salix* forest. 53°58' N, 114°06' W.	AB-93039
	ALBERTA, 4.6 km from junction of Twp. Rd. 522 and Hwy. 22, S. side of road in ditch at edge of *Populus tremuloides* and *Salix* forest, associated with *P. frigidus* var. *palmatus* and *P. sagittatus*. 53°25' N, 114°50' W.	AB-93040
	ALBERTA, 2 km W. of junction of Hwy. 759 and Hwy. 39, S. side of road near slough, in *Salix/ Picea glauca* forest, associated with *P. frigidus* var. *palmatus* and *P. sagittatus*. 53°10' N, 114°50' W.	AB-93041
	ALBERTA, Roadside at edge of *Populus tremuloides* forest, 0.7 km E. of junction of Hwy. 39 and Sec. Hwy. 777. 53°10' N, 114°30' W.	AB-93042
	ALBERTA, Grassy area at edge of *P. tremuloides, Cornus stolonifera, Salix* forest 2.1 km W. of junction of Hwy. 39 and Sec. Hwy. 795. 53°10' N, 113°50' W.	AB-93043

Note: AB, Alta; AK, Alaska; BC, British Columbia; NW, Northwest Territories; YT, Yukon Territory.

GREENHOUSE CULTIVATION

Rhizomes collected in the field were refrigerated in darkness for two months prior to planting. This cold period was applied in order to induce flowering. The purpose of this was to conduct crossing experiments between different taxa, and to test for agamospermy with the isolation of pistillate capitula. Rhizomes were planted in a mixture of sand and vermiculite in plastic trays and were placed in the greenhouse facility at the University of Alberta. Some of the seeds were also exposed to a cold period and then planted in plastic pots, in the same soil mixture as the rhizomes. Lighting was provided from natural sources. During the winter of 1991/92 plants were placed in dark refrigeration. The following spring these plants were placed outdoors.

CYTOLOGICAL STUDY

Mitotic chromosome counts were made from actively growing cells of root tips from plants that were grown in the greenhouse. Fresh root tips were collected in the morning from several individuals per population sample. They were pretreated in a solution of 0.020% colchicine (w/v) for eight hours at 4°C. After eight hours the root tips were placed in Östergreen and Heneen's fluid (Östergren and Heneen 1962) and left overnight at 4°C. They were later hydrolyzed in 1N HCl at 60°C for 8 minutes, then rinsed twice in distilled water. Then they were placed in Feulgen stain (Löve and Löve 1975) for 30 minutes. The stain was replaced, and the root tips were left for 2 to 2 1/2 hours. They were then transferred to a 2.5-3% pectinase solution for 25 minutes. Pectinase dissolves the middle lamellae of the cell walls, thereby permitting easier separation of cells, and better resolution of chromosomes. The root tips were stored for future use in 45% acetic acid at -20°C.

Root tips were prepared for visualization by using a squash technique described by Östergen and Heneen (1962). The meristematic region of each root tip was placed on a microscope slide in a drop of 45% acetic acid, macerated with a needle, then covered with a

coverslip. Pressure was then evenly applied to the coverslip. Chromosomes were observed under oil immersion with the aid of Zeiss phase contrast microscope at the University of Alberta. The temporary microscope slides were stored in a freezer at -20°C.

MORPHOLOGICAL ANALYSES

Data for the morphological studies were obtained from pressed specimens collected in the field during the first field season, and from specimens borrowed from various herbaria, including the University of Alaska (ALA), the University of Alberta (ALTA), the National Museum of Canada (CAN), the University of British Columbia (UBC), the United States National Herbarium (US), the University of Wisconsin (WIS), and Washington State University (WS). The specimens were selected to represent the entire geographical range of *Petasites*, and to reflect the morphological variability present within each taxon.

Characters selected for analyses included those most frequently utilized in keys and diagnoses of the various taxa. Additionally, characters which were considered useful in reliable identification were selected. Bogle (1961) used the bracts of the flowering stalks as an additional characters in his study of *Petasites X vitifolius*. The bracts are not included in this study because they are inconsistently present in herbarium material.

All specimens were in a mature stage of development: leaves fully expanded; anthers of the functionally staminate florets with abundant pollen; and styles of the pistillate florets elongated. The outermost phyllaries on the inflorescences were not measured, but the phyllaries next in towards the center were used. Measurements were taken with a hand ruler and an ocular micrometer in a dissecting microscope.

Leaf form is described in terms of lobes and teeth, defined as follows. A primary lobe is the leaf region separated by two sinuses. This region had to extend at least 1/4 of the distance between the leaf margin and midrib. Secondary lobes are defined as protuberances on the primary lobes which are at least 1/3 the length of the primary lobe. Teeth are defined as

protuberances of the leaf margin which are less than 1/3 the length of the primary lobes. If there are no lobes, any protuberances are considered to be teeth.

As a result of the dioecious nature of *Petasites*, and the tendency to produce short-lived reproductive inflorescences before the leaves, most specimens possessed only one kind of inflorescence, or only leaves. Therefore, it was necessary to compile separate data sets for pistillate, staminate, and leaf data. To circumvent the problem of misidentifying taxa based on flower morphology alone, only those specimens with both flowers and leaves were admitted into the pistillate or staminate data set. In most specimens, however, where both leaves and flowers were present, the leaves were in an immature stage of development and could not be included in the leaf data set. The initial data matrices were constructed from 17 vegetative characters, 25 pistillate characters, and 24 staminate characters, in addition to latitude and longitude (Tables 2-3, 2-4, and 2-5, respectively). One mature, representative leaf per plant, and one staminate or pistillate floret per head per inflorescence represented one individual. In total 271 leaves, 150 staminate florets, and 132 pistillate florets were measured for the various attributes.

Morphological variation within and among taxa of *Petasites* was assessed using univariate statistics (mean, standard deviation, variance) and multivariate morphometric analyses: discriminant analyses, and principal components analyses (PCA). Univariate statistics indicate the range of variation of each character within each taxon. A PCA can indicate which characters provide the greatest contribution to differences among taxa. It is used to show if distinct groups can be recognized without designation of *a prior* groups (Wiley 1981). In contrast, a discriminant analysis assigns individuals to groups *a priori*. It estimates the correct classification rates of the individuals assigned to these groups, and determines the discriminating characters among the different taxa.

The discriminant analyses (direct method), and univariate statitistics were generated by the SPSS program for MS-Windows, release 6.0. The subcommands DESCRIPTIVES, GROUPS, VARIABLES, STATISTICS, MISSING (individuals with missing data were included), and PLOT

Table 2-3. Morphological characters and character states for leaves of *Petasites* used in Principal Components Analysis and Discriminant Analyses. Units of measurement are enclosed in parentheses. Latitude and longitude were excluded from the Discriminant Analyses.

CHARACTERS (CHARACTER STATE)	ABBREVIATION
Shape of leaf: 1. sagittate, 2. deltoid, 3.reniform, 4. cordate-reniform, 5. cordate, 6. orbicular	SHAPE
Maximum leaf width (cm)	MAXW
Maximum leaf length (cm)	MAXL
Distance from apex to widest portion of leaf (cm)	APWID
Angle between apex and closest lobe of leaf (degrees)	APANGL
Angle between leaf base and petiole (degrees)	BAPANGL
Number of primary lobes	NO1LOB
Number of secondary lobes	NO2LOB
Apex shape of primary lobes: 1. obtuse, 1.5. intermediate, 2. acute, 3. both	LBAPSHP
Number of teeth	NOTETH
Teeth shape: 1. crenate, 2. dentate, 3. minute	TETHSHP
Depth of deepest sinus (cm)	SINDEP
Width of deepest sinus (cm)	SINWID
Base shape of deepest sinus: 1. rounded, 2. pointed	SINSHP
Perimeter of leaf (cm)	PERI
Pubescence of adaxial surface: 0. glabrous, 1. sparsely pillose, 2. velutinous, 3. floccose, 4. tomentose	PUBAD
Pubescence of abaxial surface: 0. glabrous, 1. velutinous, 2. villous, 3. floccose, 4. tomentose, 5. woolly	PUBAB
Latitude	LAT
Longitude	LONG

Table 2-4. Morphological characters and character states for staminate *Petasites* used in Principal Components Analysis and Discriminant Analysis. Units of measurement are enclosed in parentheses. Latitude and longitude were excluded from Discriminant Analyses.

CHARACTERS (CHARACTER STATE)	ABBREVIATION
Number of heads/inflorescence	NOHEADS
Phyllary width (mm)	PHYLWI
Phyllary length (mm)	PHYLLEN
Margin of phyllaries: 1. entire, 2. serrate, 2.5. intermediate	PHYLMAR
Number of ray florets/head	NORF
Position of ray florets: 1. peripheral, 2. central	POSRF
Ray length (mm)	RL
Ray width (mm)	RW
Style length (mm)	STYLEN
Length of style branches (mm)	LENSTBR
Texture of style surface: 1. papillose, 2. hairy	STYTEX
Pappus length of ray florets (mm)	PAPLENRF
Number of disc florets/head	NODF
Position of disc florets: 1. peripheral, 1.5. both, 2. central	POSDF
Corolla length (mm)	CORLEN
Corolla lobe width (mm)	CORLBWI
Style length (mm)	STYLENG
Length of style branches (mm)	LENGSTBR
Texture of style surface: 1. papillose, 1.5. intermediate, 2. hairy, 3. both	STYLTEX
Length of anthers (mm)	LENANTH
Shape of anther apical appendage: 1. round, 2. triangular, 3. both	SHPANAPP
Shape of corlla lobes: 1. rounded, 1.5. intermediate, 2. triangular, 3. both	SHPCORLB
Pappus length of disc florets (mm)	PAPLENDF
Disc corolla lobe length (mm)	DCLL
Latitude	LAT
Longitude	LONG

Table 2-5. Morphological characters and character states for pistillate *Petasites* used in Principal Components Analysis and Discriminant Analysis. Units of measurement are enclosed in parentheses. Latitude and longitude were excluded from Discriminant Analyses.

CHARACTERS (CHARACTER STATE)	ABBREVIATION
Number of heads/inflorescence	NOHEADS
Phyllary width (mm)	PHYLWI
Phyllary length (mm)	PHYLLEN
Margin of phyllaries: 1. entire, 2. serrate, 2.5. intermediate	PHYLMAR
Number of ray florets/head	NORF
Position of ray florets: 1. peripheral, 1.5. both, 2. central	POSRF
Ray length (mm)	RL
Ray width (mm)	RW
Style length (mm)	STYLEN
Length of style branches (mm)	LENSTBR
Texture of style surface: 1. papillose, 2. hairy	STYTEX
Pappus length of ray florets (mm)	PAPLENRF
Achene length (mm)	ACHLEN
Number of disc florets/head	NODF
Position of disc florets: 1. peripheral, 2. central	POSDF
Corolla length (mm)	CORLEN
Corolla lobe width (mm)	CORLBWI
Style length (mm)	STYLENG
Length of style branches (mm)	LENGSTBR
Texture of style surface: 1. papillose, 2. hairy	STYLTEX
Length of anthers (mm)	LENANTH
Shape of anther apical appendage: 1. round, 2. triangular, 3. intermediate	SHPANAPP
Shape of corolla lobes: 1. rounded, 1.5. intermediate, 2. triangular	SHPCORLB
Pappus length of disc florets (mm)	PAPLENDF
Disc corolla lobe length (mm)	DCLL
Latitude	LAT
Longitude	LONG

were used to execute these analyses. The principal components analyses were produced with the NT-SYS program, version 1.2 of Rohlf (1987). The STAND, SIMINT, EIGEN, and PROJ subcommands were employed to complete the analyses. For each data set, two discriminant analyses were computed: one with six taxonomic groups and one with four taxonomic groups. This was done to compare classification results of individuals when there were six taxa and when the entities in the var. *frigidus* complex were united. Three dimensional coordinates obtained from the discriminant analyses and PCA's were plotted by Sigmaplot, version 5.00 (Jandel Corporation 1986-1991) graphics to produce scatter diagrams.

ENZYME ANALYSIS

Horizontal starch gel electrophoresis was the method employed to assess genetic variation in *Petasites*. Material used in the electrophoretic analysis was obtained from rhizomes collected and refrigerated from the second field season, and from leaves collected from populations of *Petasites X vitifolius* in the third field season. Twenty to thirty individuals per population were used in the analysis. This is considered to be a sufficient number of individuals as it has been estimated that there is a 95% probability of detecting all alleles in a population when 30 diploid individuals are examined (Crawford 1990). Small pieces of rhizomes and 1 cm^2 pieces of fresh leaf tissue were ground in ice-cold extraction buffer (Bayer 1991) and two drops of mercaptoethanol per 10ml were added prior to use to prevent oxidation of the proteins. Supernatant was absorbed onto filter paper wicks (2 mm X 13 mm) and stored at -70^{0}C. Wicks were thawed, then loaded into 12.5% starch gels. Wicks soaked in a bromophenol blue/water solution were used as markers to indicate the migration front of the gel.

A preliminary study with numerous enzymes was performed to determine which enzymes, under various buffer systems, gave the best resolution the most consistently. Additionally, in order to ascertain which plant organ would show the most activity and best

resolution, young and mature fresh leaves and fresh and frozen rhizomes were electrophoresed on the same gel under various conditions.

The resolution of 14 enzymes was accomplished using three different gel/electrode buffer systems. The following system was used to resolve alcohol dehydrogenase (ADH), leucine aminopeptidase (LAP), phosphoglucoisomerase (PGI), and isocitrate dehydrogenase (IDH): gel buffer of one part 0.038 M lithium hydroxide monohydrate, 0.188 M boric acid (pH 8.2) and nine parts 0.045 M Tris and 0.007 citric acid (pH 8.4) (Soltis et al. 1983); the electrode buffer consisted of only the lithium borate acid component. Acid phosphatase (ACP), glucose 6-phosphate dehydrogenase (G6PDH), glutamate dehydrogenase (GDH), 6-phosphogluconic dehydrogenase (6-PGD), and diaphorase (DIA) were resolved with another system from Soltis et al. (1983): gel buffer of 0.020 M histidine hydrochloride (pH 7.0) and electrode buffer of 0.400 M citric acid trisodium salt (pH 7.0). Shikimic dehydrogenase (SKD), phosphoglucomutase (PGM), menadione reductase (MNR), malic enzyme (ME), and aldolase (ALDO) were resolved with the following system: gel buffer of 0.016 M L-Histidine (free base) and 0.002 M citric acid monohydrate (pH 6.5) and an electrode buffer of 0.065 M L-histidine (free base) and 0.007 M citric acid monohydrate (pH 6.5) (Cardy et al. 1981). Glutamate oxaloactate transaminase (GOT), esterase (EST), and catalase (CAT) exhibited no activity in *Petasites*.

Electrophoresis for the lithium borate (pH 8.3) system was conducted at 50 mA for the first hour then 60 mA for the next four hours, the histidine-HCl (pH 7.0) system was conducted at 100 mA for the first hour and 70 mA for the next four hours, and the histidine system (pH 6.5) was conducted at 40 mA for the first hour and 30 mA for the next four hours. All gels were run at 4°C and in instances when the gel was warm to the touch, crushed ice was placed upon the gel.

Most of the staining protocols followed those of Soltis et. al. (1983). The agar overlay method was used for PGI. The protocol for ADH followed that of GDH with the addition of 5 ml

of ethanol. Staining protocols for DIA, and MNR followed method 1 and method 2, respectively, of Wendel and Weeden (1989) except NADH was omitted from DIA.

Interpretation of banding patterns on gels was aided by information from Kephart (1990), Wendel and Weeden (1989), Gottlieb (1981), and Crawford (1983). The locus which migrated the most anodally was designated as 1, the next 2, and so forth. Similarly, the most anodal allozyme was designated as a, then b, and so on.

Genetic variation was evaluated using mean number of alleles per locus, including monomorphic loci (A), proportion of polymorphic loci (P), observed and expected mean number of heterozygotes (H_{obs} and H_{exp}, respectively), and mean fixation index (F_T) per population. A locus was considered to be polymorphic if the most common allele was present in a frequency of 0.99 or less (Gottlieb 1981). In a large population, genotype frequencies are predicted by Hardy-Weinberg equilibrium under the assumption of random mating, no migration, no mutation, and no selection (Hartl 1980). A chi-square test was used to test whether observed values deviated from those expected under Hardy-Weinberg equilibrium. Both 5% and 1% significance levels were used. The mean fixation index provides an indication of the degree of inbreeding in populations (Hartl 1980). A value of +1 indicates complete inbreeding, whereas a value of -1 indicates complete outcrossing. Calculations of all statistics is outlined in Hartl (1980).

Allelic frequencies were determined for all populations of *Petasites*. They were used to calculate standard genetic distances (D) and genetic identities (I) for all pair-wise comparisons of populations, and gene diversity statistics for each taxon using the methodology of Nei (1972, 1973). These statistics provide an estimate of genetic differentiation within and among populations. When two populations have the same alleles in identical frequencies, the result is a genetic identity value of 1; whereas it is zero, when they have no alleles in common (Nei 1972). Genetic distance is the negative logarithm of the genetic identity (Nei 1972). Gene diversity statistics are described by Nei (1973) with the following equations: $H_T = H_S + D_{ST}$ and G_{ST} =

D_{ST}/H_T. Total gene diversity, (H_T), is partitioned into diversity within populations (H_S) and among populations (D_{ST}). G_{ST}, the coefficient of gene differentiation, is the ratio of the among population diversity to the total diversity. Nei's statistics were calculated using the GENESTAT program, version 2.1 (Whitkus 1988).

The genetic distance data were transformed into a dissimilarity matrix using Lotus 123, version 3.1 (Lotus Development Corporation, 1989). The dissimilarity matrix was used to generate an average linkage cluster diagram using Systat, version 5.03 (Systat Inc., 1991). An average linkage cluster was chosen over a complete linkage or single linkage cluster because it tends to avoid the extremes that characterize these latter two methods. The reason for this is that the average linkage method computes an average similarity or dissimilarity between an operational taxonomic unit (OTU) and a cluster. In contrast, an OTU must have a similarity or dissimilarity equal to the farthest member or nearest member within a cluster, for complete linkage and single linkage methods, respectively (Sneath and Sokal 1973).

RESULTS

GREENHOUSE OBSERVATIONS AND CYTOLOGICAL STUDY

Plants of *Petasites* that were propagated from rhizome cuttings grew favorably in the greenhouse. The appearance of leaves from specimens in the greenhouse was compared with those from the same rhizome that were collected in the field. The number of lobes, the degree of dissection of lobes, and the number of teeth on the leaf specimens in the greenhouse were less than those that were collected in the field (unpubl. obs.).

Somatic chromosome counts were determined to be approximately $2n = 60$ for all taxa of *Petasites*. Large differences in sizes of the chromosomes were not evident. Table 2-6 lists these chromosome counts in addition to counts made from previous studies.

Packer and McPherson (1974) reported chromosome numbers of 90 for 6 population samples of var. *frigidus* from Barrow, Alaska. This evidence of triploidy was not observed in the current study, however, specimens were not examined from Barrow or other localities this far north.

MORPHOLOGICAL ANALYSES

Data Matrices

Data matrices for leaf, staminate, and pistillate characters of *Petasites* were constructed (Appendices 1, 2, and 3, respectively). The same matrices were used for both PCA and discriminant analyses, with the exception of latitude and longitude being excluded from the discriminant analyses. Latitude and longitude were removed in order to determine the most discriminating morphological characters without the influence of these two variables.

Univariate Statistics

Univariate statistics, in addition to the minumum and maximum values for each character for each taxon in *Petasites* are presented in Tables 2-7, 2-8, and 2-9 for leaf, staminate

TABLE 2-6. Chromosome numbers for populations of North American *Petasites*. Reference codes: A = current study (vouchers at ALTA); B = Taylor and Brockman (1966); C = Mosquin and Hayley (1966); D = Suda and Argus (1966); E = Johnson and Packer (1968); F = Packer and McPherson (1974); G = Löve (1975); H = Morton (1981); I = Ornduff et al. (1963); J = Sørensen and Christiansen (1964). Population designations for current study are the same as in Table 2-2.

TAXON	SOMATIC NUMBER	LOCALITY	VOUCHER SPEC.	REF-CODE
P. frigidus var. *frigidus*	60	YUKON, Klondike Loop Km 71.7	YT-92024	A
	60	YUKON, Ethel Lake campground	YT-92015	A
	60	YUKON, Keno Hill	YT-92017	A
	60	YUKON, Dempster Hwy, 1 km S. of Arctic Circle sign	YT-92023	A
	60	N.W.T., Dempster Hwy, 30 km N.of Yukon/N.W.T. border	NW-92021	A
	60	ALASKA, Taylor Hwy, 7.8 km E. of Lost Chicken Hill	AK-92028	A
	60	B.C., Yoho Nat. Park, Takakkaw Falls	4947	B
	60 ca.	N.W.T., Melville Island	6434	C
	60	ALASKA, Barrow, old beach ridge	229-66	D
	60	ALASKA, Ogotoruk Creek	s.n.	E
	60	ALASKA, Barrow	72-39	F
	60	ALASKA, Barrow	72-87	F
	60	ALASKA, Barrow	72-232	F
	60	ALASKA, Barrow	72-247	F
	60	ALASKA, Barrow	72-248	F
	60	ALASKA, Barrow	72-249	F
	60	ALASKA, Barrow	72-250	F
	60	ALASKA, Meade River	72-403	F
	60 ca.	ALASKA, Umiat	72-356	F
	90	ALASKA, Barrow	72-18	F
	90	ALASKA, Barrow	72-48	F
	90	ALASKA, Barrow	72-116	F
	90	ALASKA, Barrow	72-244	F
	90	ALASKA, Barrow	72-245	F
	90	ALASKA, Barrow	72-236	F
P. frigidus var. *palmatus*	60	B.C., Cassiar Hwy, Km 89	BC-91007	A
	60	B.C., 100 km E. of Watson Lake	BC-91044	A

TAXON	SOMATIC NUMBER	LOCALITY	VOUCHER SPEC.	REF-CODE
	60	B.C., 3.2 km S. of Iskut	BC-92008	A
	60	ALTA, Hwy 16X, 23 km W. of Edmonton	AB-92001	A
	60	YUKON, Alaska Hwy, 3 km W. of Little Rancheria Creek Bridge	YT-92014	A
	60	N.W.T., Dempster Hwy, 30 km N. of N.W.T. border	NW-92021	A
	60	MAN., near Brandon	s.n.	G
	60	ONT., Sibley Pen., Thunder Bay District	na-265	H
	60	WASH., King Co.	s.n.	I
	60	QUE., Fort Chimo	s.n.	J
	60	CALIF., Humboldt Co., Arcata	s.n.	K
P. sagittatus	60	ALTA, Edmonton, 11.4 km W. of 79 St. & Whitemud Dr.	AB-92009	A
	60	ALTA, Kinsella, U of A Ranch, 1 km S. of salt lake	AB-92005	A
	60	B.C., Alaska Hwy, 3.8 km E. of Toad R. Bridge	BC-92013	A
	60	ALASKA, Alaska Hwy, 4 km W. of Tetlin Jctn	AK-92030	A
	60	YUKON, Pine Lake	YT-92035	A
	60 ca.	B.C., Kitchener	165	B
	60	MAN., Duck Mt. Forest Preserve	5000	B
	60	WASH., Okanogan Co.	3282	I
	60	QUE., Fort Chimo	s.n.	J
Petasites X vitifolius	60	B.C., Dawson Creek, Reasebock Road	BC-91048	A
	60	ALTA., Grande Prairie, Wee Link Campground	AB-91049	A
	60 ca.	ALTA., 101 km N. of Fox Creek	AB-91050	A
	60	MAN., near Gillam	s.n.	G
	60	WASH., Kittitas Co.	s.n.	I

Table 2-7. Univariate statistics for leaf characters of *Petasites*. Included are mean, standard deviation (S.D.), and minimum and maximum values for each character. Description of character abbreviations and units of measurement are the same as in Table 2-3. Codes for taxa: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, SA = *P. sagittatus*.

				RANGE	
VARIABLE	TAXON	MEAN	S.D.	MINIMUM	MAXIMUM
SHAPE	FR	1.877	1.118	1	5
	PA	3.979	0.872	1	6
	PV	3.783	1.750	1	5
	SA	1.179	0.690	1	5
MAXW	FR	6.711	3.313	2.20	25.00
	PA	11.277	4.294	3.90	19.80
	PV	11.843	5.841	3.50	25.50
	SA	9.004	3.931	1.50	19.80
MAXL	FR	5.687	2.807	2.00	20.70
	PA	6.449	2.459	2.00	12.30
	PV	8.565	4.441	1.90	24.00
	SA	9.186	3.409	3.00	19.00
APWID	FR	6.414	3.310	1.00	23.50
	PA	8.106	3.198	2.00	16.20
	PV	10.759	5.916	1.00	32.00
	SA	12.466	12.625		
APANGL	FR	51.033	10.133	6	79
	PA	62.489	9.381	30	79
	PV	50.804	10.689	30	85
	SA	45.250	10.900	28	75
BAPANGL	FR	49.795	19.115	0	90
	PA	34.489	21.591	0	78
	PV	35.261	17.910	0	69
	SA	40.750	19.335	0	79
NO1LOB	FR	7.861	2.776	0	14
	PA	7.809	1.329	5	11
	PV	8.761	2.078	4	14
	SA	0.000	0.000	0	0
NO2LOB	FR	5.549	5.267	0	25
	PA	4.681	3.001	0	13
	PV	2.761	3.042	0	11
	SA	0.000	0.000	0	0

VARIABLE	TAXON	MEAN	S.D.	RANGE MINIMUM	RANGE MAXIMUM
LBAPSHP	FR	2.500	8.824	0	3
	PA	1.915	0.351	1	3
	PV	1.946	0.302	1	3
	SA	0.000	0.000	0	0
NOTETH	FR	8.377	5.763	0	32
	PA	21.447	11.940	0	52
	PV	15.283	9.966	0	44
	SA	32.964	13.361	0	58
TETHSHP	FR	1.697	0.641	0	3
	PA	6.170	19.786	1	3
	PV	1.957	0.419	0	3
	SA	1.804	0.724	0	3
SINDEP	FR	1.036	0.724	0.00	5.20
	PA	3.364	1.779	0.38	8.90
	PV	2.452	1.456	0.40	6.90
	SA	0.000	0.000	0.00	0.00
SINWID	FR	0.807	0.610	0.00	6.00
	PA	0.977	0.491	0.20	2.10
	PV	1.411	1.030	0.30	7.00
	SA	0.000	0.000	0.00	0.00
SINSHP	FR	1.115	0.425	0	2
	PA	1.138	0.289	1	2
	PV	1.359	0.479	1	2
	SA	0.000	0.000	0	0
PERI	FR	29.582	15.287	8.00	95.00
	PA	66.170	30.567	12.00	138.00
	PV	55.783	33.151	9.00	160.00
	SA	36.643	15.207	12.00	88.00
PUBAD	FR	1.313	1.423	0	4
	PA	0.444	0.659	0	3
	PV	0.884	1.295	0	4
	SA	2.952	1.457	0	4
PUBAB	FR	3.141	1.169	0	5
	PA	1.077	0.644	0	4
	PV	2.424	1.480	0	5
	SA	4.511	0.787	2	5

Table 2-8. Univariate statistics for characters of staminate inflorescences of *Petasites*. Included are mean, standard deviation (S.D.), and minimum and maximum values for each character. Description of character abbreviations and units of measurement are the same as in Table 2-4. Codes for taxa: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, SA = *P. sagittatus*.

				RANGE	
VARIABLE	TAXON	MEAN	S.D.	MINIMUM	MAXIMUM
NOHEADS	FR	7.320	2.937	2	20
	PA	15.512	7.047	4	32
	PV	13.364	10.033	3	32
	SA	16.130	6.553	8	35
PHYLW	FR	2.207	0.646	1.00	4.41
	PA	2.196	0.458	1.50	3.67
	PV	2.893	2.246	1.75	9.60
	SA	2.195	0.522	1.30	3.33
PHYLL	FR	7.573	1.206	3.64	10.67
	PA	7.800	1.620	5.67	12.80
	PV	7.748	1.309	6.08	10.33
	SA	7.815	0.956	6.17	9.83
PHYLMAR	FR	2.140	0.303	1.00	2.50
	PA	1.841	0.702	1.00	2.50
	PV	2.227	0.261	2.00	2.50
	SA	2.304	0.250	2.00	2.50
NORF	FR	7.507	2.384	1	13
	PA	15.976	10.910	5	70
	PV	11.182	6.416	2	27
	SA	12.043	3.948	4	19
POSRF	FR	1.047	0.204	1.0	2.0
	PA	1.012	0.078	1.0	1.5
	PV	1.000	0.000	1.0	1.0
	SA	1.000	0.000	1.0	1.0
RL	FR	5.080	1.532	1.60	12.00
	PA	4.353	1.377	0.00	6.33
	PV	5.378	1.653	2.08	7.83
	SA	5.494	1.502	1.08	7.67
RW	FR	1.682	0.761	0.10	3.75
	PA	1.141	0.777	0.00	5.00
	PV	1.967	0.785	0.80	3.50
	SA	1.777	0.707	0.92	4.40

VARIABLE	TAXON	MEAN	S.D.	RANGE MINIMUM	RANGE MAXIMUM
STYLEN	FR	6.995	1.400	2.75	10.67
	PA	6.426	1.359	1.50	10.33
	PV	6.915	1.457	4.17	8.33
	SA	6.511	1.197	4.25	8.67
LENSTBR	FR	0.302	0.179	0.10	1.50
	PA	0.210	0.094	0.08	0.60
	PV	0.245	0.081	0.14	0.40
	SA	0.216	0.106	0.01	0.48
STYTEX	FR	1.033	0.171	1.0	2.0
	PA	1.000	0.000	1.0	1.0
	PV	1.091	0.302	1.0	2.0
	SA	1.043	0.209	1.0	2.0
PAPLENRF	FR	3.682	1.297	1.00	7.50
	PA	4.000	1.108	1.92	6.25
	PV	3.884	0.840	2.08	5.17
	SA	3.693	1.126	1.75	6.25
NODF	FR	34.800	10.592	16	78
	PA	32.244	11.497	11	60
	PV	28.091	7.063	16	40
	SA	37.435	9.009	22	56
POSDF	FR	1.507	0.058	1.5	2.0
	PA	1.549	0.187	1.0	2.0
	PV	1.545	0.151	1.5	2.0
	SA	1.522	0.104	1.5	2.0
CORLEN	FR	3.907	0.589	2.44	6.08
	PA	3.751	0.447	2.64	4.83
	PV	4.475	1.847	2.80	9.80
	SA	3.692	0.832	0.36	4.58
CORLBW	FR	0.727	0.444	0.32	4.00
	PA	0.621	0.152	0.32	1.00
	PV	0.643	0.169	0.40	1.00
	SA	0.715	0.527	0.28	3.04

VARIABLE	TAXON	MEAN	S.D.	RANGE MINIMUM	RANGE MAXIMUM
SHPCORLB	FR	2.000	0.000	2	2
	PA	2.024	0.156	2	3
	PV	2.000	0.000	2	2
	SA	2.000	0.000	2	2
STYLENG	FR	9.740	2.112	3.00	15.80
	PA	9.080	2.649	5.70	23.00
	PV	9.333	2.037	5.67	11.80
	SA	9.459	1.685	5.58	13.67
LENGSTBR	FR	0.969	0.311	0.05	2.00
	PA	0.614	0.396	0.01	1.67
	PV	0.865	0.299	0.44	1.40
	SA	1.050	0.389	0.50	2.30
STYLTEX	FR	1.967	0.207	1.0	3.0
	PA	1.585	0.460	1.0	2.0
	PV	1.909	0.202	1.5	2.0
	SA	2.000	0.000	2.0	2.0
ANLEN	FR	1.946	0.368	0.52	2.92
	PA	2.076	0.572	0.04	4.16
	PV	2.092	0.399	1.20	2.64
	SA	2.139	0.439	1.40	3.83
SHPANAPP	FR	2.027	0.162	2	3
	PA	2.024	0.156	2	3
	PV	2.000	0.000	2	2
	SA	2.000	0.000	2	2
PAPLENDF	FR	4.371	1.117	1.41	6.92
	PA	4.481	1.112	1.92	8.30
	PV	4.740	0.893	3.30	6.33
	SA	3.685	0.921	2.50	6.00
DCLL	FR	1.609	0.334	0.80	2.58
	PA	2.047	0.700	0.65	3.80
	PV	1.697	0.307	1.20	2.25
	SA	1.617	0.281	1.16	2.24

Table 2-9. Univariate statistics for characters of pistillate inflorescences of *Petasites*. Included are mean, standard deviation (S.D.), and minimum and maximum values for each character. Description of character abbreviations and units of measurement are the same as in Table 2-5. Codes for taxa: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, SA = *P. sagittatus*.

				RANGE	
VARIABLE	TAXON	MEAN	S.D.	MINIMUM	MAXIMUM
NOHEADS	FR	9.903	2.888	5	19
	PA	19.727	7.739	8	42
	PV	21.636	7.672	9	34
	SA	19.563	7.294	6	34
PHYLWI	FR	2.003	0.479	1.08	3.33
	PA	1.737	0.487	0.67	2.67
	PV	1.742	0.538	1.08	2.70
	SA	1.738	0.526	1.00	3.08
PHYLLEN	FR	6.313	1.091	1.67	8.83
	PA	6.078	2.113	1.00	9.50
	PV	5.655	1.011	3.92	6.83
	SA	6.244	1.325	3.75	8.50
PHYLMAR	FR	2.160	0.235	2.00	2.50
	PA	1.788	0.674	1.00	2.50
	PV	2.227	0.261	2.00	2.50
	SA	2.250	0.258	2.00	2.50
NORF	FR	71.306	15.659	30	109
	PA	79.273	19.407	51	125
	PV	71.455	12.242	48	89
	SA	84.938	26.134	31	139
POSRF	FR	1.493	0.059	1.0	1.5
	PA	1.485	0.087	1.0	1.5
	PV	1.455	0.151	1.0	1.5
	SA	1.500	0.000	1.5	1.5
RL	FR	1.886	0.811	0.80	4.83
	PA	1.841	1.568	0.00	6.33
	PV	1.742	0.531	0.80	2.50
	SA	2.302	1.054	0.58	5.42
RW	FR	0.401	0.204	0.10	1.17
	PA	0.346	0.220	0.00	0.83
	PV	0.385	0.163	0.18	0.68
	SA	0.471	0.217	0.14	0.83

VARIABLE	TAXON	MEAN	S.D.	RANGE MINIMUM	RANGE MAXIMUM
STYLEN	FR	6.792	1.081	4.58	10.00
	PA	6.501	1.739	1.80	9.60
	PV	5.864	0.748	5.08	7.50
	SA	6.236	1.548	3.92	9.83
LENSTBR	FR	0.254	0.096	0.08	0.60
	PA	0.232	0.147	0.06	0.80
	PV	0.211	0.076	0.10	0.30
	SA	0.236	0.086	0.10	0.42
STYTEX	FR	1.014	0.118	1.0	2.0
	PA	1.000	0.000	1.0	1.0
	PS	1.000	0.000	1.0	1.0
	SA	1.000	0.000	1.0	1.0
PAPLENRF	FR	4.821	2.083	1.90	15.00
	PA	5.205	2.354	2.00	11.80
	PV	4.295	1.537	2.20	6.98
	SA	5.681	4.289	1.67	17.33
ACHLEN	FR	1.360	0.421	0.12	2.67
	PA	1.350	0.542	0.60	3.50
	PV	1.155	0.294	0.80	1.70
	SA	1.211	0.484	0.58	2.75
NODF	FR	3.028	1.644	1	12
	PA	2.182	1.185	1	5
	PV	2.182	0.982	1	4
	SA	3.000	1.155	1	5
POSDF	FR	2.000	0.000	2.0	2.0
	PA	2.000	0.000	2.0	2.0
	PV	2.009	0.030	2.0	2.0
	SA	2.006	0.025	2.0	2.0
CORLEN	FR	2.704	0.888	0.26	6.83
	PA	2.802	0.475	2.00	3.75
	PV	2.555	0.260	2.20	3.03
	SA	2.545	0.544	1.60	3.75
CORLBWI	FR	0.453	0.142	0.20	0.80
	PA	0.464	0.117	0.20	0.64
	PV	0.458	0.133	0.24	0.72
	SA	0.424	0.112	0.24	0.60

VARIABLE	TAXON	MEAN	S.D.	RANGE MINIMUM	RANGE MAXIMUM
STYLENG	FR	5.965	0.997	2.60	8.33
	PA	5.905	1.412	1.90	8.30
	PV	5.682	1.030	4.00	6.92
	SA	5,551	1.972	1.17	9.20
LENGSTBR	FR	0.554	0.226	0.00	1.24
	PA	0.342	0.188	0.00	0.80
	PV	0.553	0.240	0.34	1.20
	SA	0.621	0.221	0.26	1.32
STYLTEX	FR	1.875	0.322	1.0	2.0
	PA	1.652	0.424	1.0	2.0
	PV	1.909	0.302	1.0	2.0
	SA	2.000	0.000	2.0	2.0
LENANTH	FR	0.931	0.230	0.40	1.52
	PA	1.108	0.248	0.68	1.52
	PV	1.067	0.151	0.80	1.28
	SA	0.904	0.168	0.66	1.25
SHPANAPP	FR	2.069	0.256	2	3
	PA	2.000	0.250	1	3
	PV	2.000	0.000	2	2
	SA	2.125	0.342	2	3
SHPCORLB	FR	1.986	0.118	1.0	2.0
	PA	1.970	0.174	1.0	2.0
	PV	2.000	0.000	2.0	2.0
	SA	1.969	0.125	1.5	2.0
PAPLENDF	FR	3.735	1.291	0.50	8.33
	PA	4.168	1.400	1.67	6.91
	PV	4.177	1.273	2.02	5.67
	SA	4.085	2.309	1.80	11.33
DCLL	FR	1.206	0.542	0.36	4.40
	PA	1.674	0.501	0.52	2.88
	PV	1.338	0.370	0.80	2.04
	SA	1.118	0.426	0.40	1.84

inflorescences, and pistillate inflorescences, respectively. Values overlap extensively for all characters across all taxa.

Principal Components Analyses:

The principal components analyses for *Petasites* were computed for four taxa only. Scatter diagrams of the results from the PCA are presented for four and six taxa.

Leaves

The first three principal components accounted for 60.54% of the total variance of the data. Eigenvalues, which describe the amount of variation along its corresponding axis (Sneath and Sokal 1973), were 5.13, 4.59, and 1.78 for the first three principal components, respectively (Table 2-10). The contribution of characters is given by the loadings for that character on that component. In decreasing order, PCA 1 had highest character loadings for sinus depth, perimeter, maximum width, and pubescence on the abaxial surface. PCA 2 had highest loadings for number of teeth, maximum length, sinus shape, and distance from apex to widest portion of leaf. PCA 3 had the highest factor loadings for longitude and shape. Results from PCA 1 and PCA 2, and PCA 1 and PCA 3 were projected onto scatter diagrams. The best separation of groups was obtained when the first 2 principal components were plotted and only these results are presented here (Figs. 2-17 and 2-18).

Figure 2-17 represents this PCA with six taxa of *Petasites*. Two distinct groups are evident. One group consists of *Petasites sagittatus* and the other includes all other taxa, except for four individuals of var. *frigidus* which are closely associated with *P. sagittatus*. The similarity which unites these individuals to *P. sagitttus* is the lack of sinuses; these individuals are merely toothed. *Petasites frigidus* var. *palmatus* and *P. X vitifolius* are virtually inseparable. The var. *frigidus* complex shows slight separation from var. *palmatus* and *P. X vitifolius*. This is more

Table 2-10. Eigenvalues, percent variance, and loadings for the first 3 principal components for the leaf characters of *Petasites*. Description of character abbreviations is the same as in Table 2-3.

	PCA 1	PCA 2	PCA 3
EIGENVALUE	5.131	4.595	1.778
PERCENT VARIANCE	27.00%	24.19%	9.36%
CHARACTERS:			
SHAPE	0.555	-0.227	-0.537
MAXW	0.752	0.553	0.257
MAXL	0.436	0.724	0.446
APWID	0.476	0.720	0.394
APANGL	0.450	-0.135	-0.069
BAPANGL	-0.195	-0.175	0.258
NO1LOB	0.541	-0.679	0.212
NO2LOB	0.284	-0.361	0.439
LBAPSHP	0.568	-0.708	0.060
NOTETH	0.074	0.794	-0.088
TETHSHP	0.281	0.058	-0.108
SINDEP	0.864	-0.031	0.011
SINWID	0.575	-0.348	0.065
SINSHP	0.460	-0.719	0.043
PERI	0.819	0.434	0.155
PUBAD	-0.422	0.258	0.120
PUBAB	-0.623	0.281	0.236
LAT	-0.390	-0.512	0.504
LONG	-0.375	-0.430	0.619

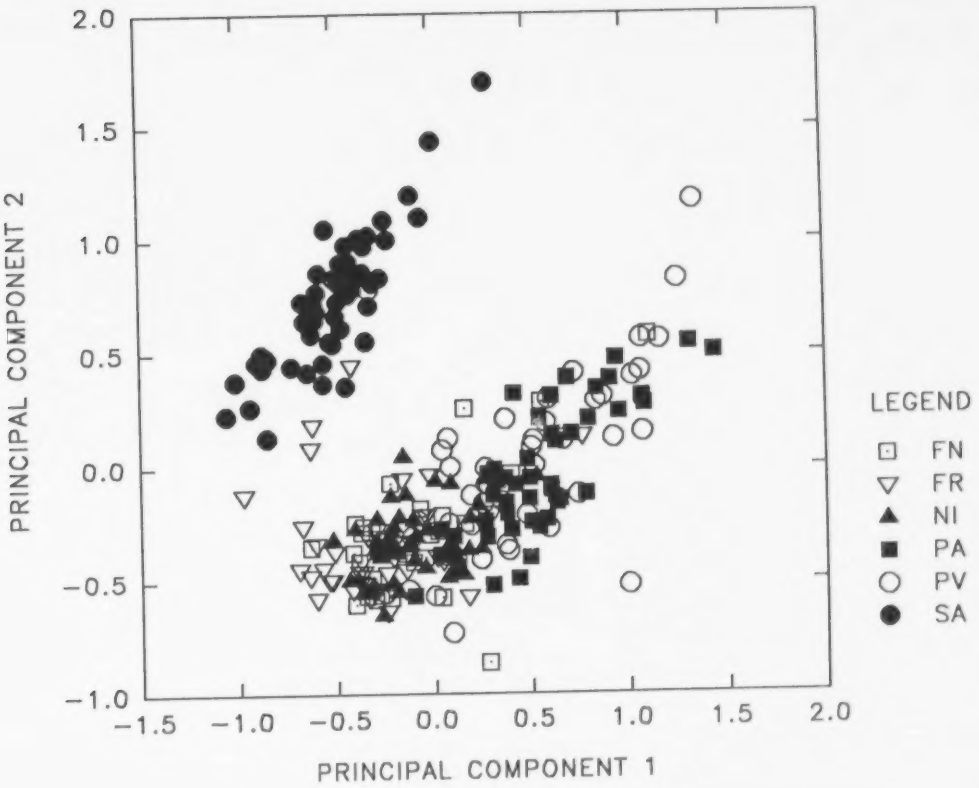

Fig. 2-17. Scatter diagram of results from Principal Components Analysis of leaf characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus* X *P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

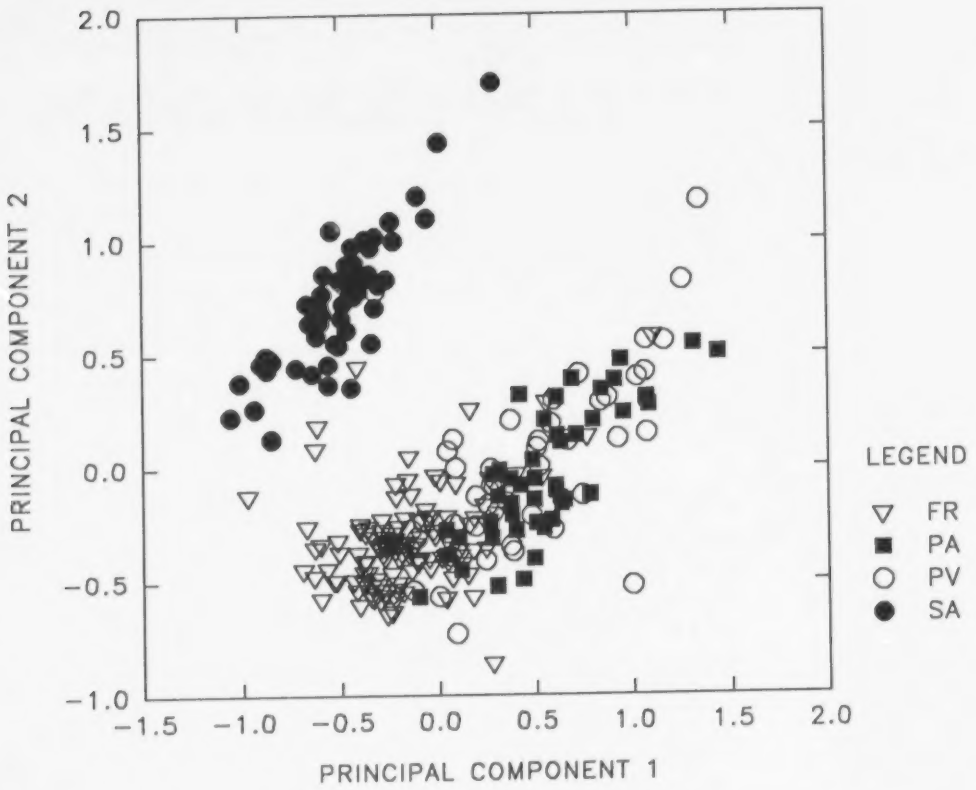

Fig. 2-18. Scatter diagram of results from Principal Components Analysis of leaf characters for four taxa of *Petasites*. Taxon codes: FR= *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

evident in Figure 2-18 when the three elements of var. *frigidus* complex are combined as one taxon, var. *frigidus*.

Staminate Inflorescences

The first three principal components accounted for 34.02% of the total variance. Eigenvalues were 3.43, 3.13, and 2.28 for the first three principal components, respectively (Table 2-11). No specific characters provided a substantial contribution to the total variance. PCA 1 had the highest loadings for ray length, style length of ray florets, texture of style of disc florets, number of heads, and latitude. PCA 2 had the highest loadings for disc corolla lobe length, pappus length of disc florets, and phyllary length. PCA 3 had the highest loadings for length of anther apical appendage and longitude. The best separation of groups occurred with the ordination of the first two principal components (Figs. 2-19 and 2-20).

No strong discontinuities exist among taxa of *Petasites* with respect to staminate inflorescences. Much overlap among all taxa occurs in the central region of the graph. Although outliers of var. *frigidus* and var. *palmatus* aid in the separation of these taxa, many members of var. *frigidus*, in addition to *P. sagittatus* and *P. X vitifolius*, are intermediate between these two extremes.

PCA 1 provides better separation of var. *frigidus* and var. *palmatus* than PCA 2 (Fig. 2-20). Ray length and latitude play a role in the distinction between var. *frigidus* and var. *palmatus* along PCA 1. *Petasites frigidus* var. *frigidus* possesses some of the longest ray lengths, whereas var. *palmatus* possesses some of the shortest (Table 2-8). Additionally, var. *frigidus* occurs at higher latitudes than var. *palmatus*. Extreme individuals of var. *palmatus* are separated from the others along PCA 2. As observed from Table 2-8, some members of var. *palmatus* possess the longest disc corolla lobes, the longest pappus of disc florets, and longest phyllaries.

Table 2-11. Eigenvalues, percent variance, and loadings of the first 3 principal components for the staminate characters of *Petasites*. Description of character abbreviations is the same as in Table 2-4.

	PCA 1	PCA 2	PCA 3
EIGENVALUE	3.428	3.131	2.285
PERCENT VARIANCE	13.18%	12.04%	8.79%
CHARACTERS:			
NOHEADS	0.537	0.298	0.349
PHYLW	0.098	-0.050	-0.218
PHYLL	-0.118	0.544	-0.172
PHYLMAR	-0.435	-0.435	0.462
NORF	0.519	0.125	0.237
POSRF	-0.061	-0.076	-0.229
RL	-0.553	0.337	0.185
RW	-0.422	-0.142	0.038
STYLEN	-0.540	0.474	-0.010
LENSTBR	-0.308	0.038	-0.215
STYTEX	-0.100	0.164	0.185
PAPLENRF	-0.395	0.487	-0.073
NODF	0.105	0.124	-0.204
POSDF	0.278	0.098	-0.365
CORLEN	-0.507	0.422	0.096
CORLBW	-0.251	0.046	-0.193
SHPCORLB	-0.005	-0.050	0.069
STYLENG	-0.387	0.419	-0.138
LENGSTBR	-0.417	-0.411	0.290
STYLTEX	-0.538	-0.485	0.422
ANLEN	-0.202	0.364	0.667
SHPANAPP	0.082	-0.031	-0.340
PAPLENDF	-0.321	0.555	-0.271
DCLL	0.098	0.614	0.156
LATITUDE	-0.534	-0.472	-0.275
LONGITUDE	-0.387	-0.285	-0.633

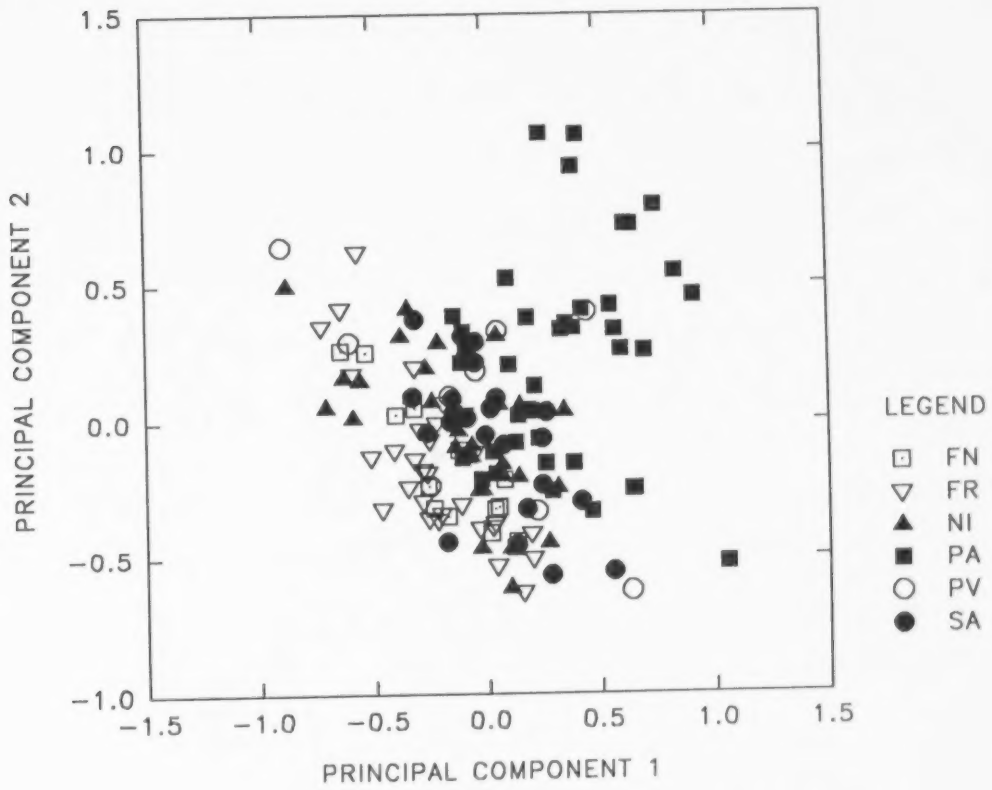

Fig. 2-19. Scatter diagram of results from Principal Components Analysis of staminate characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus X P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

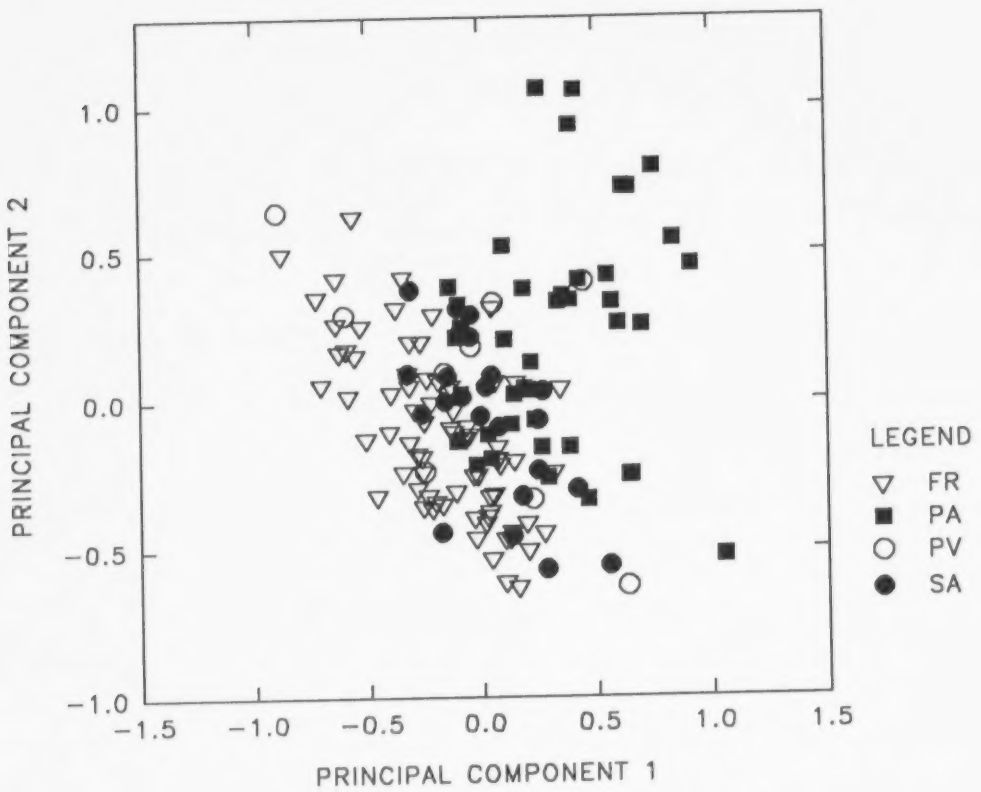

Fig. 2-20. Scatter diagram of results from Principal Components Analysis of staminate characters for four taxa of *Petasites*. Taxon codes: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

Similar to the leaf morphology, Figure 2-19 shows that the there is a large proportion of overlap among taxa of the var. *frigidus* complex. When the three elements of this complex are united the result is the formation of a more coherent group as is evident from Figure 2-20.

Pistillate Inflorescences

The first three principal components accounted for 33.46% of the total variance. Eigenvalues were 3.67, 2.98, and 2.38 for the first three principal components, respectively (Table 2-12). PCA 1 had the highest loadings for style length of ray florets, style length of disc florets, phyllary length, phyllary width, and longitude. PCA 2 had the highest loadings for ray length, the number of heads, and latitude. PCA 3 had the highest loadings for pappus length of ray florets and achene length. The ordination of PCA 1 and PCA 2 is presented in Figures 2-21 and 2-22 for six taxa and four taxa, respectively. There is virtually no separation of taxa, although extremes of var. *frigidus* and var. *palmatus* separate somewhat along PCA 2 (Fig. 2-22). This separation may be attributed to the widest range of ray length being displayed by var. *palmatus* (Table 2-5). Additionally, var. *palmatus* possesses the greatest number of heads, whereas var. *frigidus* possesses the fewest number. The role latitude plays is the same as discussed for staminate inflorescences. Separation of these two taxa is best shown in Figure 2-22. There is a weaker separation of var. *palmatus* and var. *frigidus* along PCA 1.

Discriminant Analyses

Results from the discriminant analyses computed with four taxa of *Petasites* are presented in tabular form unless otherwise indicated. Results from the discrimant analyses computed with six taxa are not presented, but are discussed in comparison to the study with four taxa.

Table 2-12. Eigenvalues, percent variance, and loadings of the first 3 principal components for the pistillate characters of *Petasites*. Description of character abbreviations is the same as in Table 2-5

	PCA 1	PCA 2	PCA 3
EIGENVALUE	3.671	2.982	2.383
PERCENT VARIANCE	13.59%	11.04%	8.83%
CHARACTERS:			
NOHEADS	0.327	0.613	-0.158
PHYLWI	-0.556	0.201	0.430
PHYLLEN	-0.611	0.228	0.015
PHYLMAR	-0.229	-0.533	0.233
NORF	0.044	0.406	0.227
POSRF	-0.318	0.137	-0.076
RL	0.024	0.689	0.405
RW	0.004	0.509	0.494
STYLEN	-0.739	0.163	-0.198
LENSTBR	-0.440	0.033	0.093
STYTEX	0.059	-0.097	-0.109
PAPLENRF	-0.440	-0.063	-0.623
SEEDLEN	-0.503	0.004	-0.545
NODF	-0.290	0.076	0.273
POSDF	-0.082	-0.035	0.017
CORLEN	-0.289	0.433	0.044
CORLBWI	-0.034	0.346	0.098
STYLENG	-0.616	0.375	-0.167
LENGSTBR	-0.452	-0.163	0.415
STYLTEX	-0.145	-0.265	0.311
LENANTH	0.072	0.270	-0.089
SHPANAPP	-0.196	-0.054	0.117
SHPCORLB	-0.121	0.086	0.217
PAPLENDF	-0.393	0.152	-0.543
DCLL	-0.043	0.514	-0.139
LATITUDE	-0.509	-0.559	0.249
LONGITUDE	-0.531	-0.195	0.283

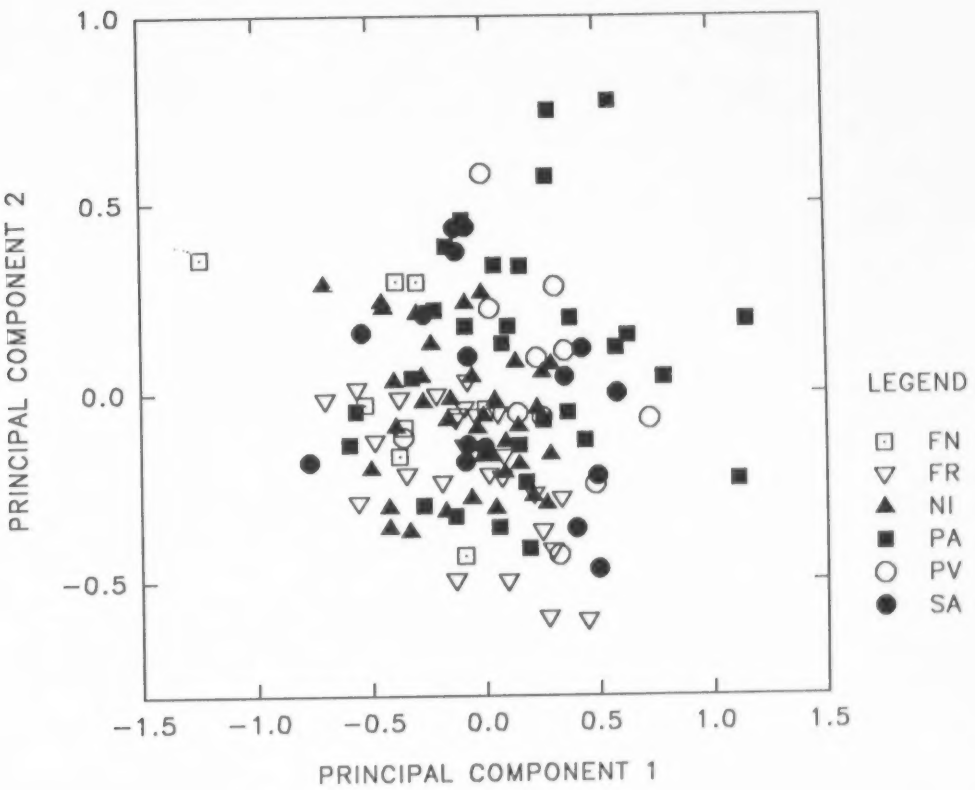

Fig. 2-21. Scatter diagram of results from Principal Components Analysis of pistillate characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus X P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

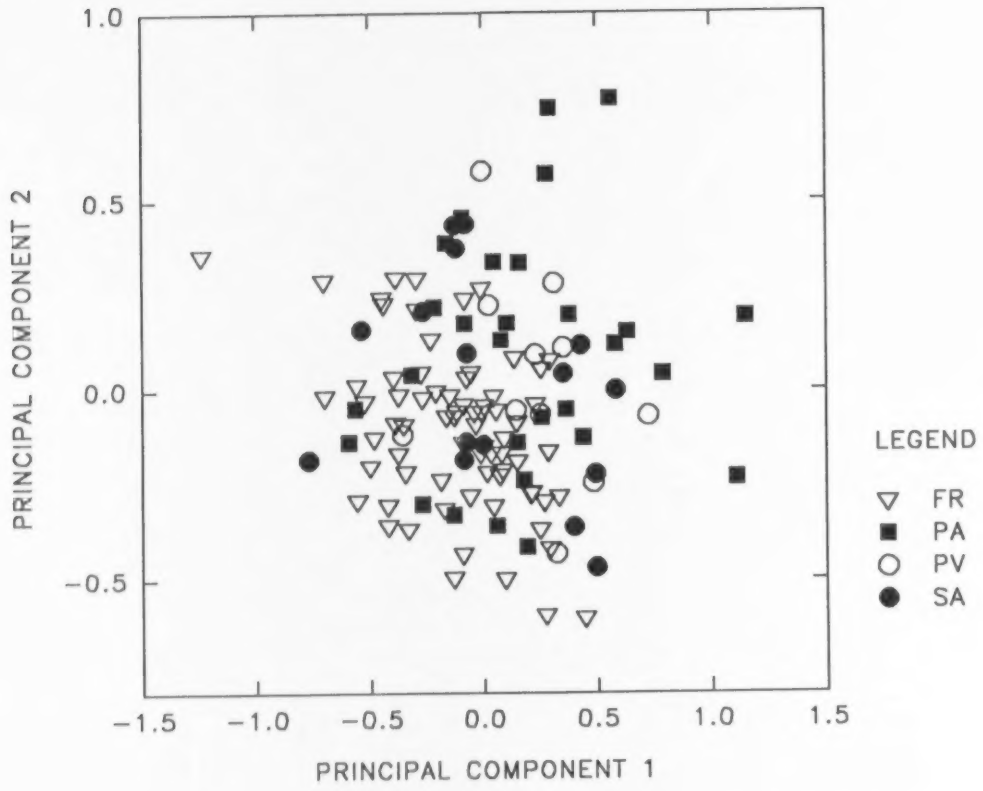

Fig. 2-22. Scatter diagram of results from Principal Components Analysis of pistillate characters for four taxa of *Petasites*. Taxon codes: FR= *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

Leaves

Results from significance tests for the equality of group means for each character are presented in Table 2-13 as F-ratios and Wilks' lambda. Wilks' lambda is the ratio of the within-groups sum of squares to the total sum of squares (Norusis 1988). Large values (close to 1) indicate that group means are not different. In contrast, small values (close to 0) indicate that group means are different, with most of the total variability attributed to differences between the group means. Characters with the highest F-ratios and corresponding lowest Wilks' lambdas are, in decreasing order, number of primary lobes, sinus shape, sinus depth, and number of teeth. Similar findings occurred in the discriminant analysis with six taxa. Group means for all characters except lobe apex shape, adaxial pubescence, and abaxial pubescence were found to be significantly different.

The first three functions accounted for 100% of the total between-groups variance in four taxa (73.59%, 20.34%, and 6.07%). Eigenvalues were 6.63, 1.83, and 0.55 for the first three discriminant functions, respectively. See Table 2-14.

The correlation coefficients between discriminating characters and canonical discriminant functions (Table 2-15) shows that the number of primary lobes, sinus shape, sinus depth, shape and number of teeth are the most discriminating characters for Function 1. These are the same characters with the highest F-ratios.

The most discriminating characters for Function 2 are also the number of teeth, sinus depth, and shape. These discriminating characters are the same characters which had the highest loadings for principal components one to three in the PCA.

The most discriminating characters for Function 3 were angle from apex to nearest lobe, sinus width, and number of secondary lobes. Several characters which also show relatively high coeffecients have not been included because they were highly correlated with one another (Appendix 4). This presupposes them to carry more weight as discriminating characters

Table 2-13. Wilks' Lambda and F-ratio obtained from the Discriminant Analysis of leaf characters of *Petasites*. Description of character abbreviations is the same as in Table 2-3.

CHARACTER	WILKS' LAMBDA	F	SIGNIFICANCE
SHAPE	0.521	81.806	0.000
MAXW	0.785	24.363	0.000
MAXL	0.820	19.509	0.000
APWID	0.881	12.050	0.000
APANGL	0.781	24.948	0.000
BAPANGL	0.893	10.669	0.000
NO1LOB	0.294	213.873	0.000
NO2LOB	0.768	26.953	0.000
LBAPSHP	0.975	2.291	0.079
NOTETH	0.505	87.361	0.000
TETHSHP	0.960	3.700	0.012
SINDEP	0.460	104.356	0.000
SINWID	0.657	46.480	0.000
SINSHP	0.364	155.648	0.000
PERI	0.702	37.759	0.000
PUBAD	0.981	1.695	0.168
PUBAB	0.991	0.816	0.486

Table 2-14. Eigenvalues, percent variance, and cumulative percent for the 3 functions for the Discriminant Analyses of leaves, pistillate inflorescences, and staminate inflorescences of *Petasites*.

MORPHOLOGICAL DATA SET	FUNCTION	EIGENVALUE	PERCENT OF VARIANCE	CUMULATIVE PERCENT
LEAVES	1	6.6308	73.59	73.59
	2	1.8308	20.34	93.93
	3	0.5468	6.07	100.00
PISTILLATE INFLORESCENCE	1	1.8276	69.82	69.82
	2	0.6223	23.78	93.60
	3	0.1675	6.40	100.00
STAMINATE INFLORESCENCE	1	2.1232	72.93	72.93
	2	0.4997	17.16	90.09
	3	0.2885	9.91	100.00

Table 2-15. Pooled within-groups correlations between discriminating leaf characters of *Petasites* and canonical discriminant functions. Characters are ordered by size of correlation within function. Description of character abbreviations is the same as in Table 2-3.

CHARACTER	FUNCTION 1	FUNCTION 2	FUNCTION 3
NO1LOB	0.5838*	-0.2754	0.0874
SINSHP	0.5009*	-0.1883	0.1928
PUBAD	-0.0520*	0.0078	0.0437
NOTETH	-0.2689	0.5233*	0.0067
SINDEP	0.3491	0.4445*	-0.0670
PERI	0.1123	0.4298*	0.0637
SHAPE	0.2912	0.4272*	0.2029
MAXW	0.0475	0.3475*	0.2618
BAPANGL	-0.0160	-0.2445*	-0.1255
LBAPSHP	0.0532	-0.0598*	-0.0269
MAXL	-0.1043	0.1946	0.3769*
APANGL	0.1518	0.1757	-0.3600*
SINWID	0.2645	0.0141	0.3258*
NO2LOB	0.1632	-0.2036	-0.3035*
APWID	-0.0877	0.1653	0.2508*
TETHSHP	0.0324	0.1116	-0.1468*
PUBAB	-0.0011	0.0005	0.1294*

* denotes largest correlation between each character and any discriminant function.

when in fact, they may not be meaningful (Norusis 1988). These characters include perimeter, maximum width, maximum length, and distance from apex to nearest lobe of leaf.

The discriminant scores of the individuals and centroids have been plotted for six taxa and for four taxa. A centroid represents the average individual computed from all the means of characters for that particular taxon. Results from Function 1 and Function 2 are presented because they account for most of the variation and displayed the best separation of taxa. Figures 2-23 and 2-24 show the results for six taxa. Figures 2-25 and 2-26 show the results when only four taxa are recognized. There is much better separation of taxa here than occurred in the PCA. Three groups are evident. *Petasites sagittatus* appears to be the most distinct. The two other groups, the var. *frigidus* complex and var. *palmatus* and *P. X vitifolius*, are more weakly defined (Fig. 2-23). *Petasites sagittatus* is best separated from the other taxa along Function 1, whereas the var. *palmatus* and the *P. X vitifolius* group separate from the var. *frigidus* complex predominately along Function 2.

The separation of *P. sagittatus* from the other taxa along Function 1 is mostly due to a lack of lobes and sinuses. As occurred in the PCA, the absence of lobes in some individuals of var. *frigidus* places them closer to *P. sagittatus* than to other members of var. *frigidus*.

The possession of the fewest number of teeth (0-32; Table 2-7) and the shallowest sinuses (0-5.20 mm) segregates the var. *frigidus* complex from the other taxa. The possession of the deepest sinuses in var. *palmatus* and *P. X vitifolius* (0.38-8.90 and 0.40-6.90, respectively) promotes their close association. Additionally, being the only taxon with orbicular shaped leaves, var. *palmatus* is further removed from the other taxa.

The overlapping range of character values within the var. *frigidus* complex illustrates the morphological similarity among its three entities. Within the var. *frigidus* complex (not shown in table), values for number of primary lobes were 3-14, 0-12, and 5-13 for var. *frigidus* (*sens. strict.*), *P. frigidus* var. *frigidus X P. frigidus* var. *nivalis*, and var. *nivalis*, respectively. Similarly, values for sinus shape were 1-2, 0-2, and 1-2. Values for sinus depth were 0.5-4 cm, 0-1.6 cm,

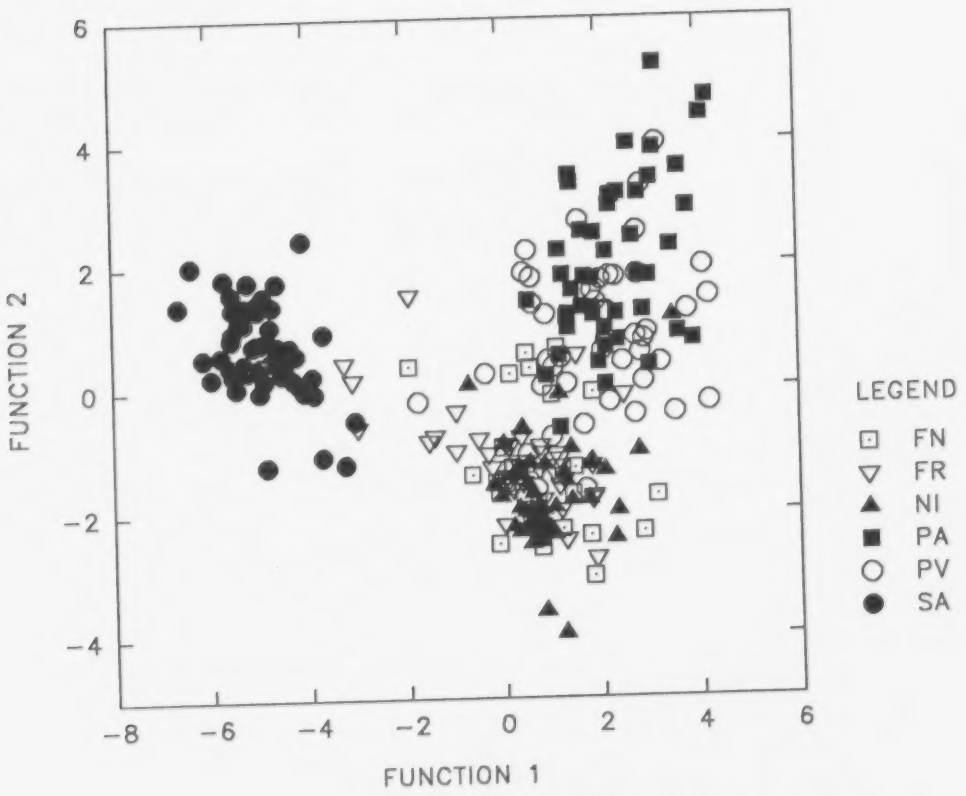

Fig. 2-23. Scatter diagram of results from Discriminant Analysis of leaf characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus* X *P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

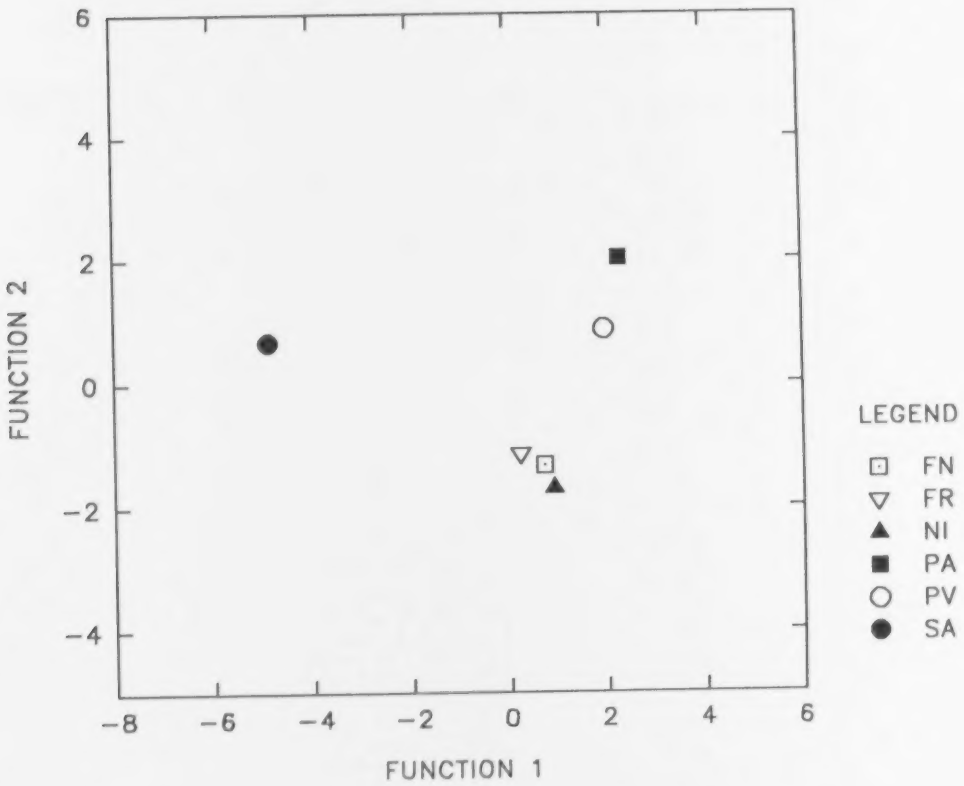

Figure 2-24. Scatter diagram of centroids from Discriminant Analysis of leaf characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus* X *P. frigidus* var. *nivalis*, FR = *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

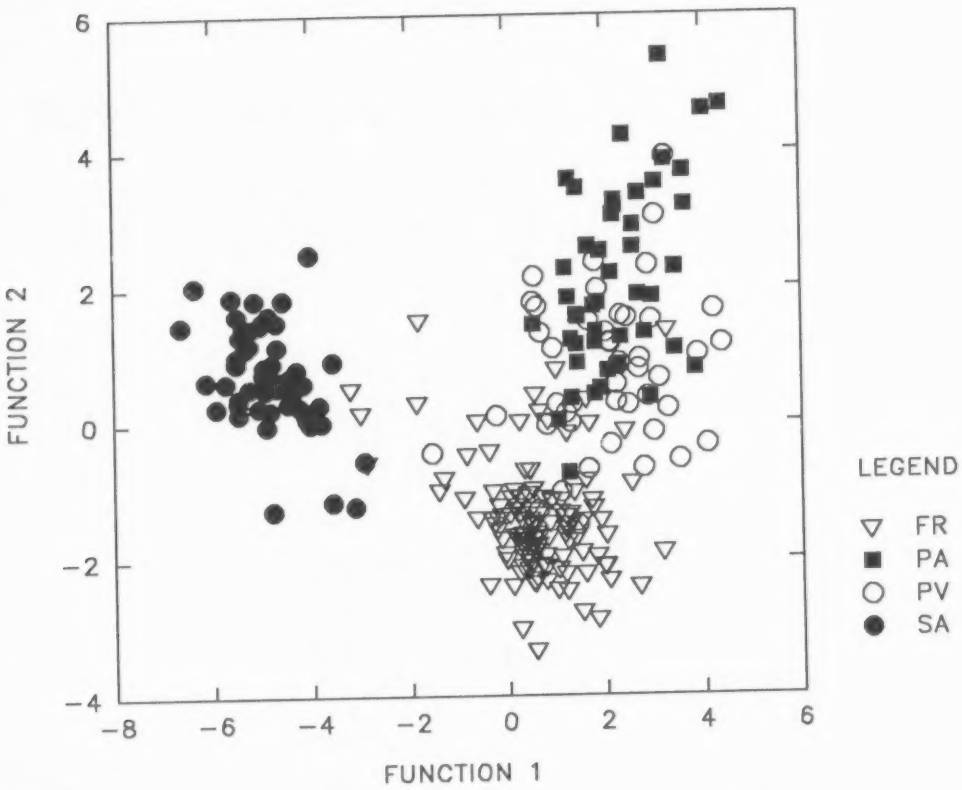

Fig. 2-25. Scatter diagram of results from Discriminant Analysis of leaf characters for four taxa of *Petasites*. Taxon codes: FR= *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

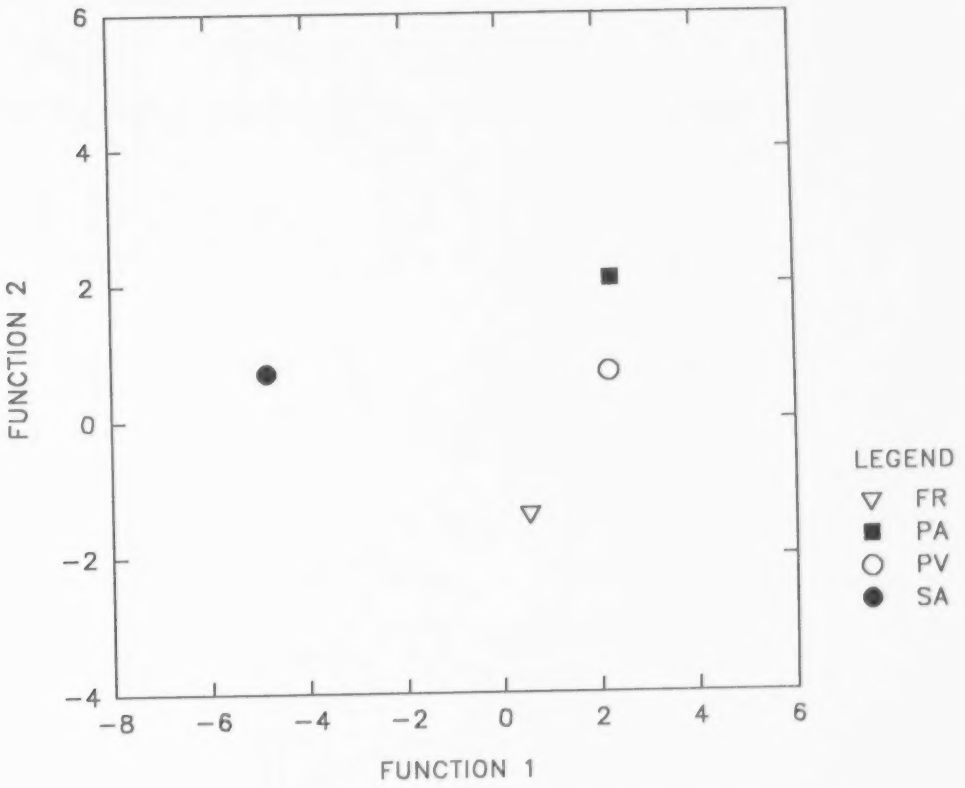

Fig. 2-26. Scatter diagram of centroids from Discriminant Analysis of leaf characters for four taxa of *Petasites*. Taxon codes: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

and 0.14-5.2 cm. Values for shape were all 1 to 5 (sagittate to orbicular) for entities of the var. *frigidus* complex. Lastly, values for number of teeth were 2-32, 0-22, and 3-32.

Upon examination of the centroids, in Figure 2-24, the proximity of the entities of the var. *frigidus* complex is visualized and supports their unification. Figure 2-26 portrays the effectiveness of such an amalgamation. The var. *frigidus* complex becomes a coherent, more convincing group when recognized collectively as var. *frigidus*.

Classification results for four taxa are presented in Table 2-16. *Petasites frigidus* var. *frigidus* had a correct classification rate of 88.5%. Although most misclassified individuals of *Petasites frigidus* var. *frigidus* were assigned to *P. X vitifolius*, only a few were assigned to var. *palmatus*.

The results for the var. *frigidus* complex, from the discriminant analysis for six taxa (not shown in table), were: 35.5% of the intermediates were correctly classified, 72.7% of var. *frigidus* were correctly classified, and 66.0% of var. *nivalis* were correctly classified. The intermediates were misclassified as var. *frigidus* in 29.0% of the cases, as var. *nivalis* and *P. X vitfolius* in 16.1% of the cases, and as var. *palmatus* in 3.2% of the cases. *Petasites frigidus* var. *frigidus* was misclassified as the intermediates in 13.6% of the cases, as *P. sagittatus* in 9.1% of the cases, and as *P. X vitifolius* in 4.5% of the cases. *Petasites frigidus* var. *nivalis* was misclassifed as var. *frigidus* in 17% of the cases, as the intermediates in 14.9% of the cases, and as var. *palmatus* in 2.1% of the cases.

Petasites frigidus var. *palmatus* had a correct classification rate of 85.1% (Table 2-16). *Petasites frigidus* var. *palmatus* was misclassified either as *P. X vitifolius* or as var. *frigidus*. The discriminant analysis with six taxa predicted a correct classification rate of 83.0% for var. *palmatus*. In this analysis, *Petasites frigidus* var. *palmatus* was misclassified as *P. X vitifolius* in 8.5% of the cases, as var. *frigidus* in 6.4% of the cases, and as var. *nivalis* in 2.1% of the cases.

Table 2-16. Classification results from the discriminant analysis for leaves of *Petasites*. Taxon codes: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, SA = *P. sagittatus*. Overall correct classification rate is 88.9%.

ACTUAL TAXON	NUMBER OF CASES	PREDICTED GROUP MEMBERSHIP			
		FR	PA	PV	SA
FR	122	108 88.5%	2 1.6%	8 6.6%	4 3.3%
PA	47	3 6.4%	40 85.1%	4 8.5%	0 0.0%
PV	46	5 10.9%	4 8.7%	37 80.4%	0 0.0%
SA	56	0 0.0%	0 0.0%	0 0.0%	56 100.0%

Petasites X vitifolius had a correct classification rate of 80.4% (Table 2-16). This hybrid was misclassified either as var. *frigidus* or as var. *palmatus*. The discriminant analysis with six taxa correctly classified *P. X vitifolius* in 76.1% of the cases. *Petasites X vitifolius* was misclassified as both var. *frigidus* and var. *palmatus* in 8.7% of the cases, as the intermediates in 4.3% of the cases, and as var. *nivalis* in 2.2% of the cases.

All individuals of *Petasites sagittatus* were correctly classified (Table 2-16). Only 4/122 individuals of var. *frigidus* were incorrectly classified as *P. sagittatus*. This taxon appears to be the most distinct morphologically. Similar results were obtained with the recognition of six taxa.

The overall rate of correct classification of four taxa was 88.9%. This rate decreased to 75.3% when six taxa were recognized.

Staminate Inflorescences

Results from significance tests for the equality of group means for each character are presented in Table 2-17. Characters with the highest F-ratios and corresponding low Wilks' lambda are, in decreasing order, number of heads, style texture of disc florets, number ray florets, and length of style branches of disc florets. Similar findings occurred in the discriminant analysis with six taxa. The characters that had significantly different group means in addition to those above mentioned were disc corolla lobe length, phyllary margin, ray width, length style branches of ray florets, ray length, pappus length of disc florets, and corolla length.

The first three functions accounted for 100% of the total variance in the four taxa analysis. Eigenvalues were 2.12, 0.49, and 0.29 for the first three discriminant functions, respectively (refer to Table 2-14).

The correlation coefficients between discriminating characters and canonical discriminant functions (Table 2-18) indicate the number of heads, the number of ray florets, and style texture of disc florets are the most discriminating variables for Function 1. These characters also have high F-ratios.

Table 2-17. Wilks' Lambda and F-ratios obtained from the Discriminant Analysis of staminate characters of *Petasites*. Description of character abbreviations is the same as in Table 2-4.

CHARACTER	WILKS' LAMBDA	F	SIGNIFICANCE
NOHEADS	0.647	26.574	0.000
PHYLW	0.952	2.476	0.064
PHYLL	0.992	0.372	0.773
PHYLMAR	0.878	6.791	0.000
NORF	0.753	15.977	0.000
POSRF	0.982	0.917	0.434
RL	0.930	3.674	0.014
RW	0.883	6.478	0.000
STYLEN	0.963	1.863	0.139
LENSTBR	0.915	4.510	0.005
STYTEX	0.980	0.998	0.396
PAPLENRF	0.986	0.698	0.555
NODF	0.950	2.544	0.059
POSDF	0.976	1.215	0.306
CORLEN	0.939	3.183	0.026
CORLBW	0.985	0.744	0.528
SHPCORLB	0.982	0.884	0.451
STYLENG	0.984	0.810	0.490
LENGSTBR	0.809	11.468	0.000
STYLTEX	0.731	17.891	0.000
ANLEN	0.969	1.542	0.206
SHPANAPP	0.994	0.295	0.829
PAPLENDF	0.931	3.602	0.015
DCLL	0.847	8.800	0.000

Table 2-18. Pooled within-groups correlations between discriminating staminate characters of *Petasites* and canonical discriminant functions. Characters are ordered by size of correlation within function. Description of character abbreviations is the same as in Table 2-4.

CHARACTER	FUNCTION 1	FUNCTION 2	FUNCTION 3
NORF	-0.3897*	0.1045	-0.0356
STYLTEX	0.3843*	0.3288	0.0101
DCLL	-0.2778*	-0.1843	-0.0090
LENSTBR	0.1884*	-0.1850	0.0254
STYLEN	0.1222*	-0.0846	0.1021
POSDF	-0.1034*	0.0134	0.0872
STYLENG	0.0878*	-0.0128	-0.0262
SHPCORLB	-0.0862*	-0.0655	-0.0302
CORLBW	0.0802*	0.0244	-0.0683
PAPLENRF	-0.0779*	-0.0379	0.0512
NOHEADS	-0.4352	0.5366*	-0.0227
PHYLMAR	0.1923	0.3454*	0.0704
LENGSTBR	0.2953	0.3096*	-0.0962
RL	0.1381	0.2584*	0.0757
RW	0.2030	0.2515*	0.2201
ANLEN	-0.0878	0.1744*	0.0194
POSRF	0.0689	-0.1273*	-0.0477
SHPANAPP	0.0065	-0.1047*	-0.0416
PHYLL	-0.0516	0.0634*	0.0005
CORLEN	0.0566	-0.0220	0.4498*
PHYLW	-0.0007	0.0747	0.4082*
NODF	0.0734	0.1156	-0.3441*
PAPLENDF	-0.0290	-0.2979	0.3109*
STYTEX	0.0557	0.1056	0.1702*

* denotes the largest correlation between each character and any discriminant function.

The number of heads and style texture of disc florets are the only characters common to both the discriminant analysis and PCA that were indicated to have provided a large contribution to the total variance. *Petasites frigidus* var. *frigidus* possesses the fewest number of heads (2-20) and fewest number of ray florets (1-13) whereas var. *palmatus* possesses the highest number of ray florets (5-70) and a moderate number of heads (4-32). Refer to Table 2-8. *Petasites sagittatus* has the highest number of heads (8-35) and a relatively low number of ray florets (4-19). *Petasites X vitifolius* possesses values which are intermediate those for *P. sagittatus* and var. *palmatus* for these characters.

The most discriminating characters for Function 2 are number of heads, phyllary margin, style texture of disc florets, and length of style branches of disc florets. *Petasites sagittatus* is best separated from the other taxa along Function 2. As previously mentioned *P. sagittatus* has the highest number of heads in addition to a consistently hairy style texture of disc florets, and the longest style branches of disc florets (0.50-2.30; Table 2-18).

For Function 3, corolla length, phyllary width, and number of disc florets are the most discriminating characters. Style texture of disc florets and phyllary margin are moderately correlated (0.56; Appendix 5) so their value as discriminating characters may not be as important as they appear. Style texture of disc florets and the number of heads are the only characters common to both the discriminant analysis and PCA that were indicated to have provided a large contribution to the total variance.

Staminate character values within the var. *frigidus* complex are highly overlapping, as occurred with the leaf characters. Within the var. *frigidus* complex, values for the number of heads (not shown in table) are 3-13, 3-12, and 2-20 for var. *frigidus* (*sens. strict.*), *P. frigidus* var. *frigidus X* var. *nivalis*, and var. *nivalis*, respectively. Similarly, values for number of ray florets are 5-12, 1-13, and 2-12. Values for style texture of disc florets is 1.5-2, 1.5-2, and 1.0-3.0. Values for phyllary margin are 2-2.5, 2-2.5, and 1-2.5. Lastly, values for length of style branches of disc florets is 0.76-2.00 mm, 0.06-1.6, and 0.05-1.40 mm.

The ordination of the discriminant scores of the individual cases and centroids for six and four taxa is shown in Figures 2-27 to 2-30. Results from Function 1 and Function 2 showed the best separation of taxa, therefore they are presented here.

Figures 2-27 and 2-28 show the results for six taxa. Three weakly defined groups can be distinguished: *Petasites frigidus* var. *palmatus*, the var. *frigidus* complex, and *P. sagittatus*. *Petasites X vitifolius* does not form a cohesive group but is scattered throughout the loose groups of the other taxa. *Petasites frigidus* var. *palmatus* is best separated from *P. sagittatus* and the var. *frigidus* complex along Function 1. *Petasites sagittatus* is best separated from the other taxa along Function 2. As previously mentioned *P. sagittatus* has the highest number of heads in addition to a consistently hairy style texture of disc florets, and the longest style branches of disc florets (0.50-2.30; Table 2-8). The position of the centroids (Figs. 2-28 and 2-30) shows that, morphologically, *P. X vitifolius* occupies a relatively intermediate position between var. *palmatus* and *P. sagittatus*. This is congruent with the concept that a hybrid is morphologically intermediate to its parents.

Similar to the leaf results, the close association of the centroids in the var. *frigidus* complex supports their unification (Fig. 2-28). Figures 2-29 and 2-30 show the result after such a unification, when only four taxa are recognized.

Classification results for four taxa are presented in Table 2-19. *Petasites frigidus* var. *frigidus* had a correct classification rate of 86.7%. Most misclassified individuals of var. *frigidus* were assigned to *P. sagittatus* and *P. X vitifolius*, whereas only a few were assigned to var. *palmatus*.

The results for the var. *frigidus* complex (not shown in table) from the discriminant analysis for six taxa, were: 66.7% of the intermediates in the var. *frigidus* complex were correctly classified, 58.6% of var. *frigidus* were correctly classified, and 58.1% var. *nivalis* were correctly classified. Intermediates were misclassified as both var. *frigidus* and var. *nivalis* in 13.3% of the cases, and as *P. sagittatus* in 6.7% of the cases.

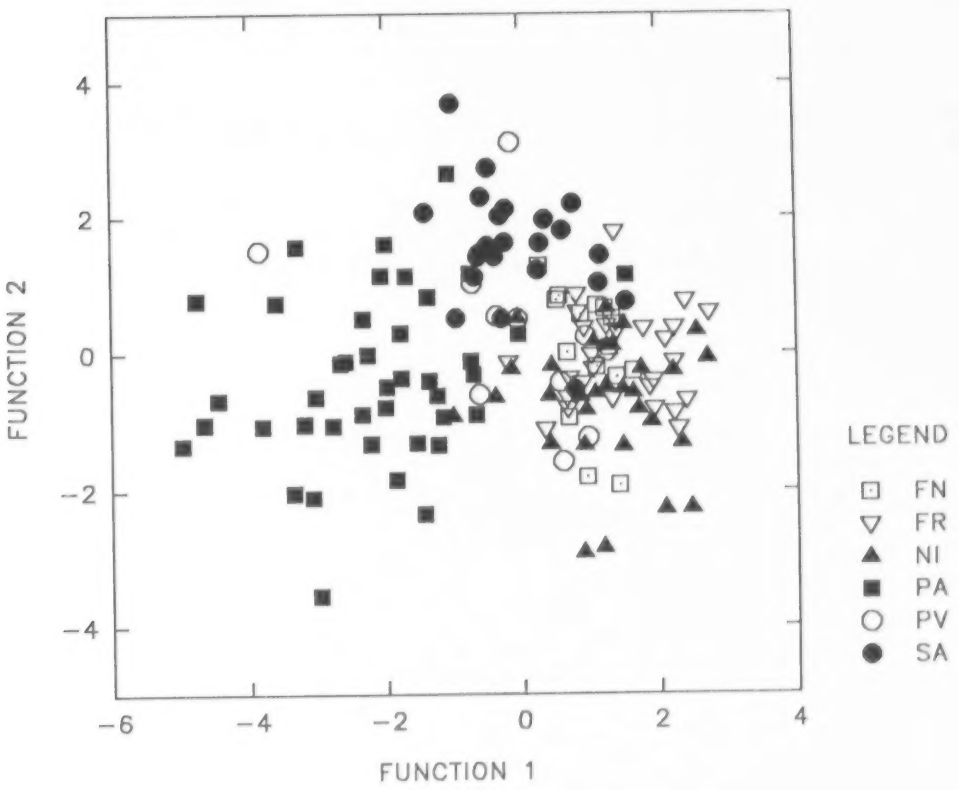

Fig. 2-27. Scatter diagram of results from Discriminant Analysis of staminate characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus* X *P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

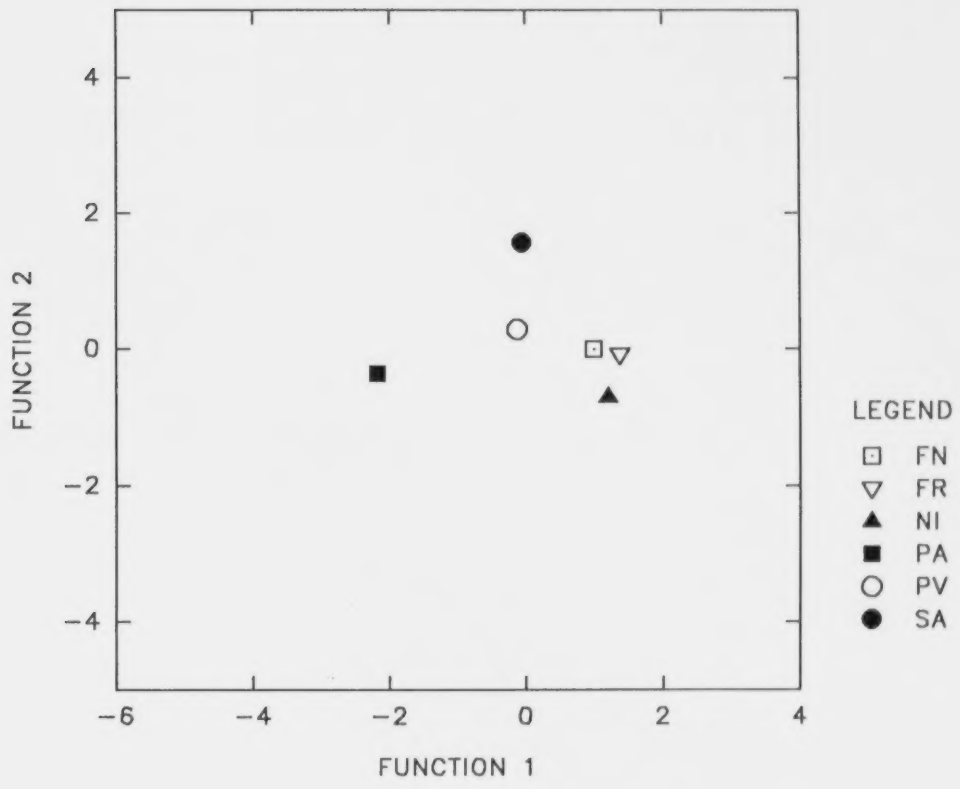

Figure 2-28. Scatter diagram of centroids from Discriminant Analysis of staminate characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus X P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

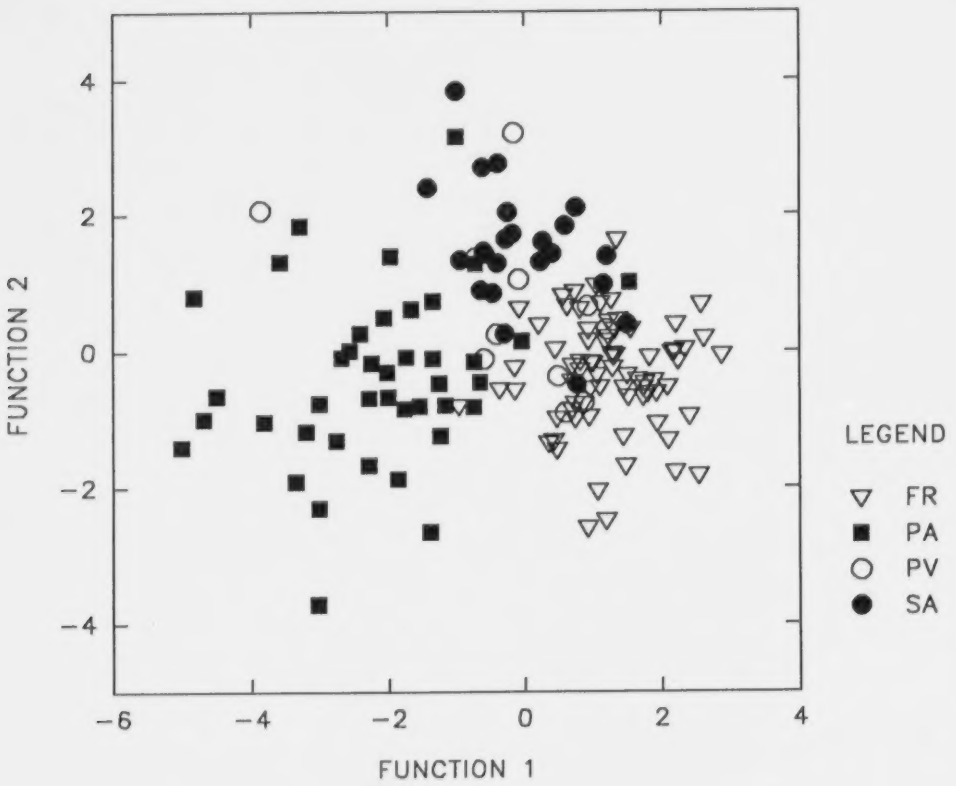

Figure 2-29. Scatter diagram of results from Discriminant Analysis of staminate characters for four taxa of *Petasites*. Taxon codes: FR= *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

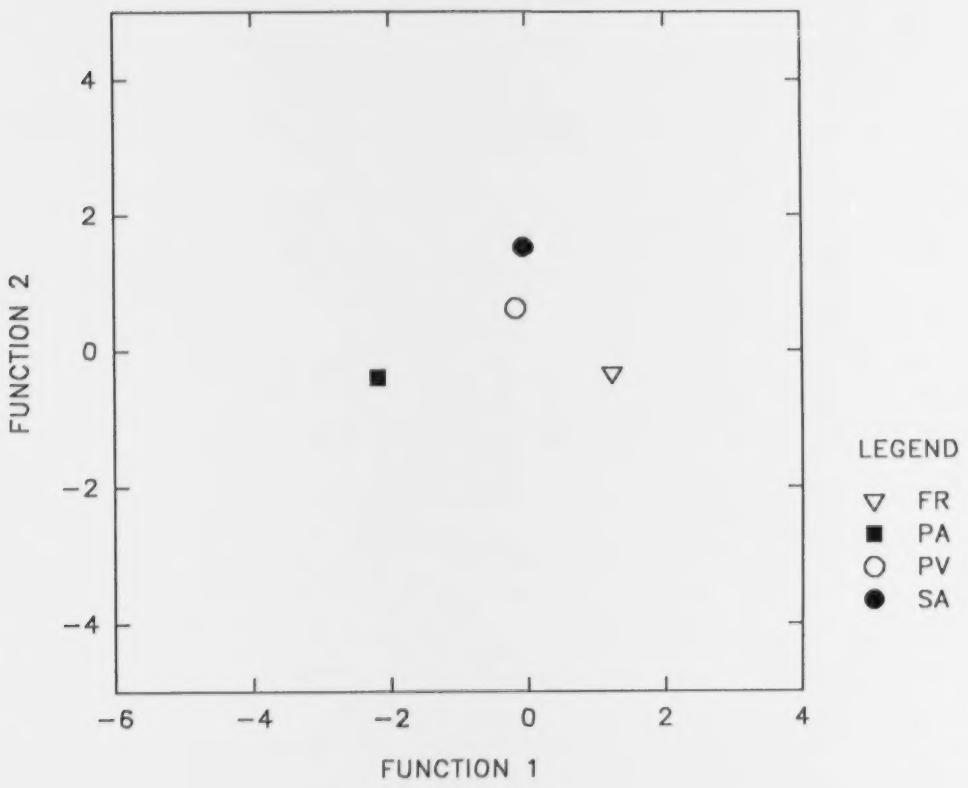

Figure 2-30. Scatter diagram of centroids from Discriminant Analysis of staminate characters for four taxa of *Petasites*. Taxon codes: FR= *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

Table 2-19. Classification results from discriminant analysis for staminate *Petasites*. Taxon codes: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, SA = *P. sagittatus*. Overall correct classification rate is 83.3%.

ACTUAL TAXON	NUMBER OF CASES	PREDICTED TAXON MEMBERSHIP			
		FR	PA	PV	SA
FR	75	65 86.7%	1 1.3%	4 5.3%	5 6.7%
PA	41	2 4.9%	35 85.4%	2 4.9%	2 4.9%
PV	11	2 18.2%	1 9.1%	6 54.5%	2 18.2%
SA	23	2 8.7%	0 0.0%	2 8.7%	19 82.6%

Petasites frigidus var. *palmatus* had a correct classification rate of 85.4% (Table 2-19). Misclassification rates of var. *palmatus* as the other three taxa were all equal at 4.9%. The discriminant analysis with six taxa correctly classified var. *palmatus* in 85.4% of the cases. *Petasites frigidus* var. *palmatus* had a misclassification rate of 4.9% for both the intermediates and *P. sagittatus*, and 2.4% for var. *frigidus* and *P. X vitifolius*.

Petasites X vitifolius had a correct classification rate of 54.5% (Table 2-19). Equal numbers of misclassified individuals of *Petasites X vitifolius* were assigned to var. *frigidus* and *P. sagittatus*. Only one individual was misclassifed as var. *palmatus*. The discriminant analysis for six taxa (not shown in table) predicted a correct classification rate of 54.5% for *P. X vitifolius*. *Petasites X vitifolius* was misclassified as *P. sagittatus* in 18.2 % of the cases. *Petasites frigidus* var. *frigidus*, var. *nivalis*, and var. *palmatus* all had misclassification rates of 9.1%.

Petasites sagittatus had a correct classification rate of 82.6% (Table 2-19). Equal numbers of misclassified individuals of *P. sagittatus* were misclassified as var. *frigidus* and *P. X vitifolius*. The results from the discriminant analysis for six taxa were identical (not shown in table).

The overall rate of correct classification of four taxa was 83.33%. This rate was reduced to 70% when six taxa were recognized.

Pistillate Inflorescences

Results from significance tests for the equality of group means for each character are presented in Table 2-20. Characters with the highest F-ratios and corresponding low Wilks' lambda are, in decreasing order, number of heads, length of style branches of disc florets, phyllary margin, and disc corolla lobe length. The number of heads is by far the most important character of these, as indicated by its high F-ratio. Similar findings occurred in the discriminant analysis with six taxa. The other characters that had significantly different group means include

Table 2-20. Wilks' Lambda and F-ratio obtained from the Discriminant Analysis of pistillate characters of *Petasites*. Description of character abbreviations is the same as in Table 2-5.

CHARACTER	WILKS' LAMBDA	F	SIGNIFICANCE
NOHEADS	0.534	37.171	0.000
PHYLWI	0.931	3.180	0.027
PHYLLEN	0.982	0.760	0.518
PHYLMAR	0.835	8.430	0.000
NORF	0.926	3.421	0.019
POSRF	0.977	0.997	0.397
RL	0.980	0.875	0.456
RW	0.969	1.376	0.253
STYLEN	0.953	2.117	0.101
LENSTBR	0.984	0.697	0.556
STYTEX	0.994	0.273	0.845
PAPLENRF	0.979	0.898	0.444
SEEDLEN	0.976	1.029	0.382
NODF	0.928	3.323	0.022
POSDF	0.977	0.988	0.410
CORLEN	0.986	0.598	0.618
CORLBWI	0.992	0.339	0.797
STYLENG	0.987	0.567	0.638
LENGSTBR	0.825	9.053	0.000
STYLTEX	0.891	5.237	0.002
LENANTH	0.878	5.934	0.001
SHPANAPP	0.974	1.148	0.333
SHPCORLB	0.994	0.243	0.866
PAPLENDF	0.980	0.871	0.458
DCLL	0.852	7.416	0.000

anther length, style texture of disc florets, number of ray florets, number of disc florets, and phyllary width.

The first three functions accounted for 100% of the total variance in four taxa (69.82%, 23.78%, and 6.40%). Eigenvalues were 1.83, 0.62, and 0.17 for the first three discriminant functions, (refer to Table 2-14).

The correlation coeffiecients between discriminating characters and canonical discriminant functions (Table 2-21) shows the number of heads, length of style branches of disc florets, disc corolla lobe length, and phyllary margin for Function 1. These are the same characters with the highest F-ratios. For Function 2 the number of heads, length of style branches of disc florets, phyllary margin, and style texture of disc florets are the most discriminating characters. The most discriminating characters for Function 3 include the number of ray florets, pappus length of ray florets, and position of ray florets. The number of heads and pappus length of ray florets are the only characters common to both the discriminant and PCA that were indicated to have provided a high contribution to the total variance. Correlation coefficients of pistillate characters are available in Appendix 6.

The ordination of the discriminant scores of the individual cases and centroids for six and four taxa is shown in Figures 2-31 to 2-34, respectively. Results from Function 1 and Function 2 showed the best separation of taxa, therefore they are presented here. In Figure 2-31, four weakly defined groups are evident: var. *palmatus*, *P. sagittatus*, *P. X vitifolis*, and the var. *frigidus* complex. The best separation of var. *palmatus* and the other taxa occurs along Function 1.

The values for the most discriminating character along Function 1 and Function 2 are presented for the various taxa. Referring back to Table 2-9, var. *frigidus* possesses the fewest number of heads (5-19) whereas var. *palmatus* possesses the highest number of heads (8-42). *Petasites sagittatus* and *P. X vitifolius* exhibit values that are intermediate between the former

Table 2-21. Pooled within-groups correlations between discriminating pistillate characters of *Petasites* and canonical discriminant functions. Characters are ordered by size of correlation within function. Description of character abbreviations is the same as in Table 2-5.

	FUNCTION 1	FUNCTION 2	FUNCTION 3
NOHEADS	-0.6077*	0.5616	-0.0255
DCLL	-0.2710*	-0.2198	0.0553
LENANTH	-0.2611*	-0.1231	-0.1738
NODF	0.1992*	0.0333	0.1663
PHYLWI	0.1789*	-0.1570	-0.0649
PAPLENDF	-0.0982*	0.0671	0.0055
STYTEX	0.0523*	-0.0465	-0.0174
LENGSTBR	0.2823	0.3150*	-0.1700
PHYLMAR	0.2620	0.3030*	-0.2991
STYLTEX	0.1916	0.2928*	-0.1164
STYLEN	0.0971	-0.2065*	0.1867
SEEDLEN	0.0275	-0.1785*	0.1318
RW	0.0832	0.1694*	0.1019
STYLENG	0.0226	-0.1408*	-0.0124
CORLEN	-0.0295	-0.1356*	0.0762
CORLBWI	-0.0275	-0.0916*	-0.0891
NORF	-0.1205	0.1839	0.4409*
PAPLENRF	-0.0298	0.0638	0.3177*
POSRF	0.0599	-0.0157	0.3154*
RL	0.0232	0.1318	0.2280*
PHYLLEN	0.0710	-0.0475	0.2075*
POSDF	0.0286	0.1586	-0.1894*
SHPANAPP	0.0943	0.0973	0.1688*
SHPCORLB	0.0290	-0.0070	-0.1567*
LENSTBR	0.0783	-0.0711	0.1093*

* denotes largest correlation between each variable and any discriminant function.

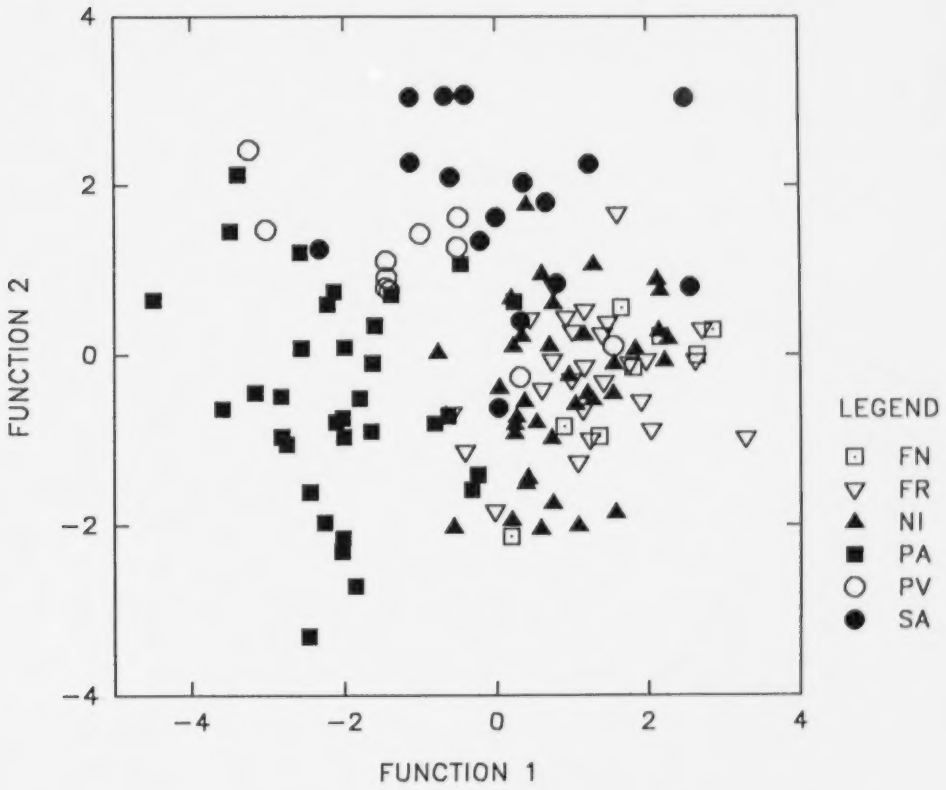

Figure 2-31. Scatter diagram of results from Discriminant Analysis of pistillate characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus* X *P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

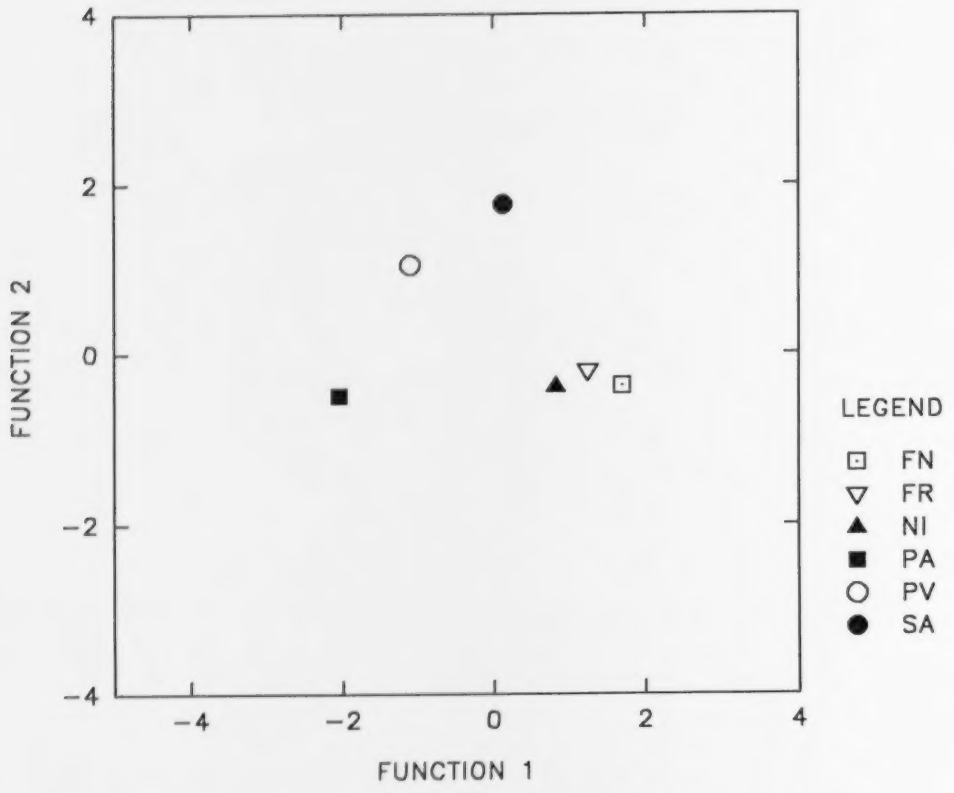

Figure 2-32. Scatter diagram of centroids from Discriminant Analysis of pistillate characters for six taxa of *Petasites*. Taxon codes: FN = *P. frigidus* var. *frigidus* X *P. frigidus* var. *nivalis*, FR= *P. frigidus* var. *frigidus*, NI = *P. frigidus* var. *nivalis*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

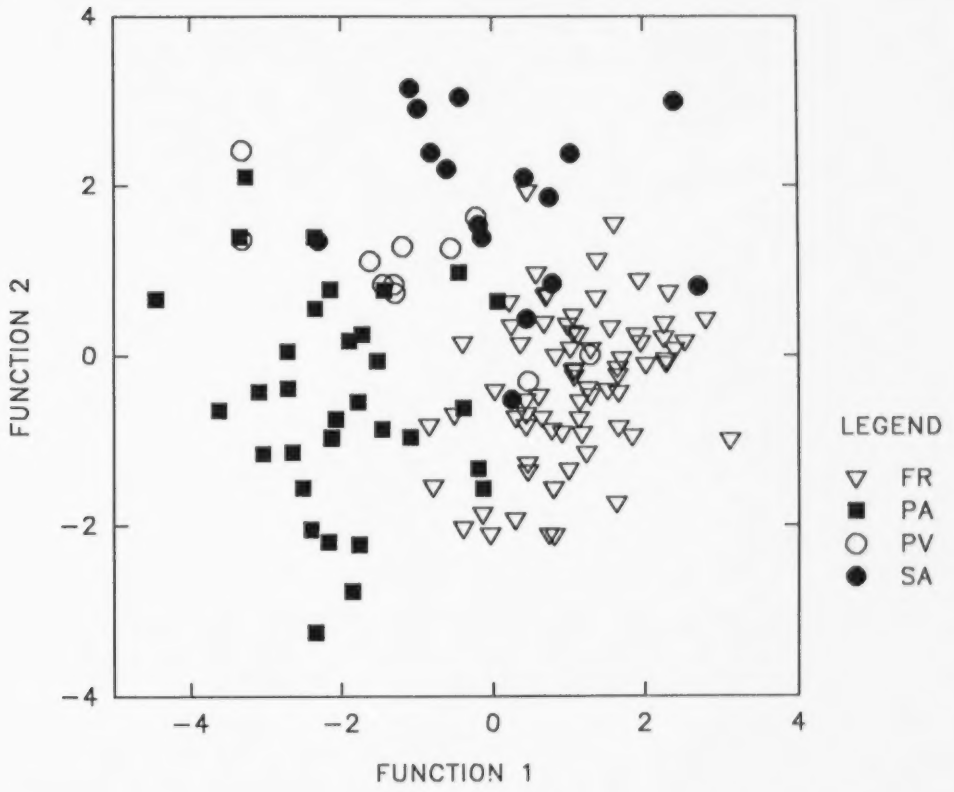

Figure 2-33. Scatter diagram of results from Discriminant Analysis of pistillate characters for four taxa of *Petasites*. Taxon codes: FR= *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

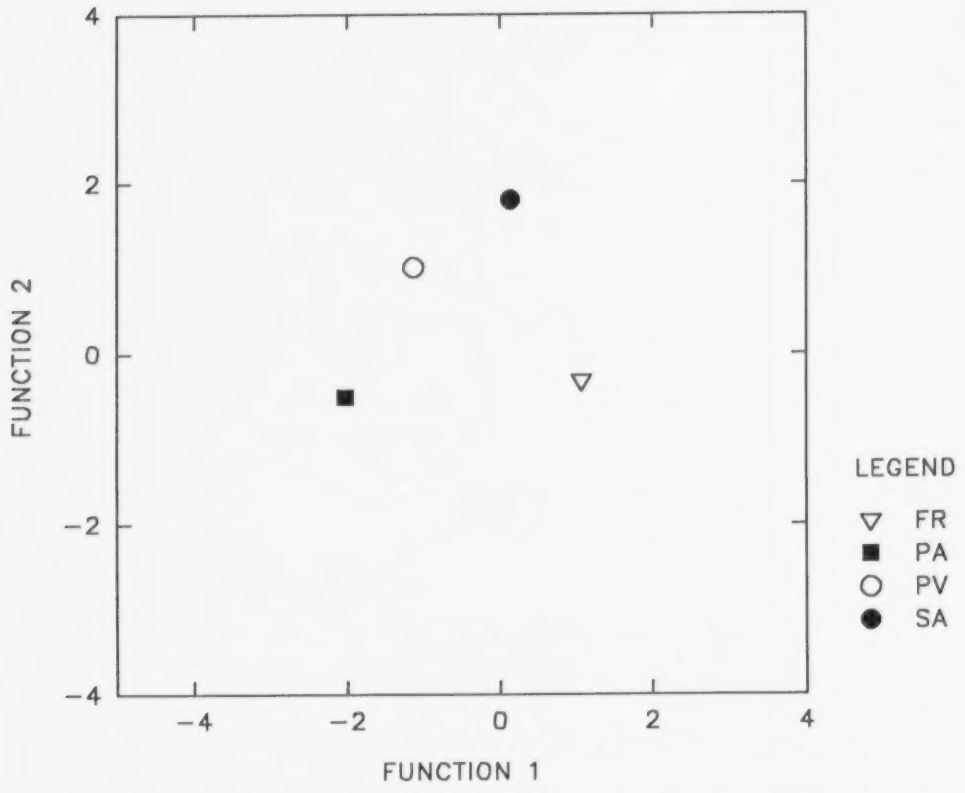

Figure 2-34. Scatter diagram of centroids from Discriminant Analysis of pistillate characters for four taxa of *Petasites*. Taxon codes: FR= *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

two taxa. *Petasites sagittatus* exhibits the longest style branches of disc florets (0.26-1.32 mm). The largest disc corolla lobe length occurs in var. *frigidus* (0.36-4.40 mm) and the smallest occurs in *P. sagittatus* (0.40-1.84 mm). The phyllary margin in var. *palmatus* is distinguished from the other taxa by the presence of completely entire phyllary margins in some individuals.

The centroids of the six taxa (Fig. 2-32) indicate the presence of four groups. The close association of the three entities of the var. *frigidus* complex favors the amalgamation of these entities into one taxon. The result of this combination is shown in Figures 2-33 and 2-34.

Classification results for four taxa are presented in Table 2-22. *Petasites frigidus* var. *frigidus* had a correct classification rate 87.5%. Although most misclassified individuals of *Petasites frigidus* var. *frigidus* were assigned to *P. sagittatus*, only a few were assigned to *P. X vitifolius* and var. *palmatus*.

The results for the var. *frigidus* complex from the discriminant analysis (not shown in table) with six taxa, were: 75% of the intermediates were correctly classified, 76.9% of var. *frigidus* were correctly classified, and 76.3% of var. *nivalis* were correctly classified. The intermediates were misclassified only as var. *frigidus* in 25% of the cases. *Petasites frigidus* var. *frigidus* was misclassified as var. *nivalis* in 11.5% of the cases, as the intermediates in 7.7% of the cases, and as *P. sagittatus* in 3.8% of the cases. *Petasites frigidus* var. *nivalis* was misclassified as *P. sagittatus* in 10.5% of the cases, as var. *frigidus* in 7.9% of the cases, and as the intermediates and *P. X vitifolius* in 2.6% of the cases.

Petasites frigidus var. *palmatus* had a correct classification rate of 75.8% (Table 2-22). Misclassified individuals of this variety were assigned either as *P. X vitifolius* or as var. *frigidus*. The discriminant analysis with six taxa (not shown in table) predicted a correct classification rate of 72.7% for var. *palmatus*. This taxon was misclassified as *P. X vitifolius* in 15.2% of the cases, as var. *nivalis* in 9.1% of the cases, and as the intermediates in 3% of the cases.

Table 2-22. Classification results from discriminant analysis for pistillate *Petasites*. Taxon codes: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, SA = *P. sagittatus*. Overall correct classification rate is 80.3%.

ACTUAL TAXON	NUMBER OF CASES	PREDICTED TAXON MEMBERSHIP			
		FR	PA	PV	SA
FR	72	63 87.5%	1 1.4%	2 2.8%	6 8.3%
PA	33	3 9.1%	25 75.8%	5 15.2%	0 0.0%
PV	11	2 18.2%	1 9.1%	8 72.7%	0 0.0%
SA	16	4 25.0%	1 6.3%	1 6.3%	10 62.5%

Petasites X vitifolius had a correct classification rate of 72.7% of the cases (Table 2-22). Misclassified individuals of this hybrid were assigned to either var. *frigidus* or var. *palmatus*. The discriminant analysis with six taxa produced the same results (not shown in table). *Petasites X vitifolius* was misclassifed as vars. *frigidus*, *nivalis*, and *palmatus* in 9.1% of the cases.

Petasites sagittatus had a correct classification rate of 62.5% (Table 2-22). Although most misclassified individuals of *Petasites sagittatus* were assigned to var. *frigidus*, only one individual was assigned to var. *palmatus* and *P. X vitifolius*. The correct classification rate of *P. sagittatus* in the discriminant analysis with six taxa was also 62.5% (not shown in table). The misclassification rates of *P. sagittatus* were 18.8% as var. *nivalis*, and 6.3% as the intermediates, var. *palmatus*, and *P. X vitifolius*. The overall rate of correct classification of four taxa was 80.3%. This rate decreased to 73.5% when two additional taxa were recognized.

ENZYME ANALYSIS

Eleven enzyme systems assayed are interpreted as being encoded by 22 loci. Three enzyme systems, DIA, ALDO,, and ME, were not used in the analysis because they were not interpretable. Additionally, as a result of inadequate resolution, MNR-1, PGM-1, and IDH-2 were also omitted. The 19 isozymes (and their allozymes) used in the analysis include: GDH-1 (A), 6PGD-1 (A), 6PGD-2 (A to D), G6PDH-1 (A and B), G6PDH-2 (A to D), ACP-1 (A), ACP-2 (A), LAP-1 (A and B), LAP-2 (A to C), ADH-1 (A to F), ADH-2 (A to F), IDH-1 (A), PGI-1 (A), PGI-2 (A to F), SKDH-1 (A to C), SKDH-2 (A to C), PGM-2 (A to C), PGM-3 (A and B), and MNR-2 (A).

The number of isozymes for each enzyme system is highly conserved among diploid plants (Gottlieb 1982). The number of isozymes in *Petasites* is in close agreement with reports for other diploid plants (Bayer 1992, Gottlieb 1982, Kephart 1990, Weeden and Wendel 1989).

Segregation at polymorphic loci provides evidence for determining the subunit composition of enzymes. The subunit composition of the enzymes used in this study are in agreement with results from Gottlieb (1981), Weeden and Wendel (1989), and (Kephart 1990).

Monomeric enzymes include ACP, SKDH (Weeden and Wendel 1989, Kephart 1990), PGM (Gottlieb 1981, Weeden and Wendel 1989, Kephart 1990, Hashemi and Estilai 1992), and LAP (Gottlieb 1981, and Kephart 1990). Dimeric enzymes include 6PGD (Gottlieb 1981 and Kephart 1990), ADH, PGI (Gottlieb 1981, Weeden and Wendel 1989, and Kephart 1990), G6PDH, and IDH (Weeden and Wendel 1989 and Kephart 1990). MNR is considered to be a tetramer (Hashemi and Estilai 1992). Weeden and Wendel (1989) and Kephart (1990) consider GDH to be a hexamer.

A table of allelic frequencies for *Petasites* is provided in Appendix 7. Seven isozymes were monomorphic for identical alleles in all 47 populations: GDH-1, 6PGD-1, ACP-1, ACP-2, IDH-1, PGI-1, and MNR-2. All populations of *P. X vitifolius* were monomorphic for 6PGD-2 D and ADH-1 C. All taxa shared the same high frequency allele at 5 out of 12 polymorphic loci (G6PDH-1 A, LAP-1 A, LAP-2 A, PGM-2 B, and PGM-3 A). Two unique alleles were observed in *P. frigidus* var. *frigidus*. Allele *6Pgd-2*^{a} was present in moderately high frequencies (0.18 to 0.50) in six populations of var. *frigidus*, while allele *Adh-2*^{e} was present in very low frequencies (0.02 and 0.03) in only two populations. Several alleles were shared by only two taxa. *Adh-1*^{a} and *Adh-1*^{e} were present only in *P. sagittatus* and var. *frigidus*, *Adh-2*^{b} was present in var. *frigidus* and var. *palmatus*, *Adh-2*^{f} was present in var. *frigidus* and *P. X vitifolius*, and *Skdh-1*^{a} was present in *P. X vitifolius* and var. *palmatus*.

Genetic variation in 47 populations of *Petasites* is presented in Table 2-23 as mean number of alleles per locus (*A*), proportion of polymorphic loci (*P*), observed and expected proportion of loci heterozygous (H_{obs} and H_{exp}, respectively), and mean fixation indices (F_T). The values of *A* range from 1.37 to 1.94 for var. *frigidus* with a mean of 1.61. The values of *A* for var. *palmatus* range from 1.2 to 1.71 with a mean of 1.44. The values of *A* for *P. sagittatus* extend from 1.00 (all loci monomorphic) to 1.83, with a mean of 1.43. For *P. X vitifolius* the values of *A* range from 1.37 to 1.79 with a mean of 1.58. For all taxa the values of *A* range from 1.00 to 1.94 with a mean of 1.54. Values of *P* range from 0.30 to 0.0.63 with a mean of

TABLE 2-23. Genetic variation within *Petasites*. Included are: mean number of alleles per locus (*A*); proportion of polymorphci loci (*P*); observed proportion of loci heterozygose (H_{obs}); expected proportion of loci heterozygose (H_{exp}); and mean fixation index (F_T). * = significantly different at the 5% level; ** = significantly different at the 1% level. Population designations are as in Table 2-2.

POP. DESIG.	*A*	*P*	H_{obs}	H_{exp}	F_T
Petasites frigidus var. *frigidus*					
AK-92026	1.69 ± 0.92	0.4375	0.1553	0.1618	0.041
AK-92027	1.75 ± 0.75	0.6250	0.2232	0.2395	0.068
AK-92028	1.84 ± 1.14	0.4737	0.1968	0.2141	0.081
AK-92029	1.82 ± 1.15	0.4706	0.2062	0.1822	-0.132
AK-92031	1.94 ± 1.22	0.4444	0.2266	0.2241	-0.011
AK-92032	1.42 ± 0.67	0.3158	0.1506 **	0.0980	-0.536
AK-92033	1.53 ± 0.82	0.3684	0.2156 **	0.1606	-0.343
AK-92034	1.83 ± 1.12	0.5000	0.2154	0.2034	-0.059
NW-92021	1.41 ± 0.49	0.4118	0.1909 **	0.1331	-0.434
NW-92022	1.58 ± 0.88	0.3684	0.1753	0.1392	-0.259
YT-92015	1.68 ± 0.92	0.4211	0.1285	0.1567	0.180
YT-920161	1.38 ± 0.60	0.3125	0.1739 **	0.1072	-0.624
YT-920162	1.44 ± 0.49	0.4444	0.2941 **	0.1872	-0.571
YT-92017	1.63 ± 0.98	0.4211	0.1416 **	0.2612	0.458
YT-92018	1.41 ± 0.60	0.3529	0.2008 **	0.1342	-0.496
YT-92019	1.37 ± 0.48	0.3684	0.2354 **	0.1614	-0.459
YT-92020	1.59 ± 0.60	0.5294	0.2442 **	0.1927	-0.267
YT-92023	1.47 ± 0.85	0.2941	0.1704	0.1341	-0.271
YT-92024	1.68 ± 0.98	0.4737	0.2258	0.1943	-0.163
YT-92025	1.76 ± 1.06	0.4118	0.2500 **	0.1852	0.600
YT-92036	1.80 ± 0.91	0.5333	0.1138	0.1425	0.201
YT-92037	1.47 ± 0.62	0.4000	0.0982 *	0.1417	0.307
AVERAGE	**1.61 ± 0.17**	**0.4263**	**0.1924**	**0.1707**	**0.122**
± SD		0.0779	0.0471	0.0409	0.333
Petasites frigidus var. *palmatus*					
AB-92001	1.20 ± 0.40	0.2000	0.0487	0.0378	-0.290
AB-92002	1.38 ± 0.60	0.3125	0.0424 **	0.1231	0.655
AB-92003	1.44 ± 0.70	0.3125	0.1247	0.0992	-0.258
AB-92004	1.41 ± 0.97	0.2353	0.0338 **	0.0950	0.644
AB-92008	1.27 ± 0.45	0.2727	0.0278 **	0.1154	0.759
BC-92010	1.35 ± 0.59	0.2941	0.1111	0.1162	0.082
BC-92012	1.47 ± 0.70	0.3529	0.1382	0.1254	-0.102
NW-92021	1.41 ± 0.60	0.3529	0.1627	0.1326	-0.228
NW-92022	1.58 ± 0.75	0.4211	0.1654	0.1474	-0.122

POP. DESIG.	*A*	*P*	H_{obs}	H_{exp}	F_T
YT-92014	1.65 ± 0.90	0.3529	0.1434 **	0.0834	-0.719
YT-92023	1.71 ± 0.89	0.4706	0.1549	0.1861	0.168
AVERAGE	**1.44 ± 0.15**	**0.3252**	**0.1048**	**0.1147**	**0.054**
± SD		0.0741	0.0527	0.0359	0.444
Petasites *sagittatus*					
AB-92005	1.33 ± 0.58	0.2778	0.0414 **	0.0916	0.548
AB-92006	1.00 ± 0.00	0.0000	0.0000	0.0000	-
AB-92007	1.15 ± 0.36	0.1538	0.0941 *	0.0471	-1.000
AB-92009	1.40 ± 0.61	0.3333	0.0134 **	0.0561	0.761
AK-92030	1.83 ± 1.17	0.4444	0.1518	0.1838	0.174
BC-92011	1.31 0.58	0.2500	0.1062	0.1106	0.040
BC-92013	1.65 ± 0.90	0.3529	0.1434 **	0.0834	0.292
YT-92035	1.72 ± 0.99	0.4444	0.1994	0.1847	-0.079
AVERAGE	**1.43 ± 0.27**	**0.2821**	**0.0937**	**0.0947**	**0.092**
± SD		0.1403	0.0662	0.0604	0.492
Petasites X vitifolius					
AB-93038	1.68 ± 0.92	0.4211	0.0859 **	0.1243	0.309
AB-93039	1.59 ± 0.75	0.4211	0.1307	0.1274	-0.026
AB-93040	1.79 ± 1.06	0.4737	0.1793	0.1639	-0.094
AB-93041	1.37 ± 0.58	0.3158	0.1503 *	0.1189	-0.265
AB-93042	1.37 ± 0.58	0.3158	0.1043	0.0991	-0.053
AB-93043	1.68 ± 0.80	0.4737	0.1414 *	0.1863	0.241
AVERAGE	**1.58 ± 0.16**	**0.4035**	**0.1320**	**0.1367**	**0.019**
± SD		0.0656	0.0304	0.0294	0.197
GRAND AVERAGE	**1.54 ± 0.20**	**0.3833**	**0.1506**	**0.1433**	**-0.027**
± SD		0.0924	0.0637	0.0488	0.395

0.43 for var. *frigidus*. For var. *palmatus* values of *P* range from 0.20 to 0.47 with a mean of 0.33. Values of *P* for *P. sagittatus* range from 0.00 (all loci monomorphic) to 0.44 with a mean of 0.28. For *P. X vitifolius* values of *P* range from 0.32 to 0.47 with a mean of 0.40. The range and mean of *P* over all taxa is 0.00 to 0.63 and 0.38, respectively.

The chi-square analysis is a test of the null hypothesis that the observed heterozygosities do not differ significantly from those predicted by Hardy-Weinberg equilibrium. The observed and expected heterozygosities were not significantly different from Hardy-Weinberg expectations in just over half of the cases. The values of H_{obs} for var. *frigidus* ranged from 0.10 to 0.30 with a mean of 0.19. For var. *palmatus* values of H_{obs} ranged from 0.03 to 0.17 with a mean of 0.11. The values of H_{obs} for *P. sagittatus* ranged from 0.00 to 0.20 with a mean of 0.20. For *P. X vitifolius* values of H_{obs} ranged from 0.09 to 0.18 with a mean of 0.13. Over all taxa H_{obs} ranged from 0.00 to 0.29 with a mean of 0.13. Values of H_{exp} for var. *frigidus* ranged from 0.10 to 0.26 with a mean of 0.17. Values of H_{exp} for var. *palmatus* ranged from 0.04 to 0.19 with a mean of 0.12. For *P. sagittatus* values of H_{exp} ranged from 0.00 to 0.19 with a mean of 0.10. For *P. X vitifolius* values of H_{exp} ranged from 0.10 to 0.16 with a mean of 0.14. For all taxa values of H_{exp} ranged from 0.00 to 0.26 with a mean of 0.14.

The range and mean for the mean fixation index (F_T) for var. *frigidus* is -0.62 to 0.60 and 0.12, respectively. F_T ranges from -0.72 to 0.08 and has a mean of 0.05 for var. *palmatus*. For *Petasites sagittatus* F_T has a range of -1.00, indicating complete outcrossing, to 0.55 with a mean of 0.09. *Petasites X vitifolius* has a range of -0.27 to 0.31 and a mean value of 0.02 for F_T. Overall taxa the range and mean value of F_T is -1.00 to 0.60 and -0.03, respectively.

Gene diversity statistics for individual and pooled taxa of *Petasites* are presented in Table 2-24. PGI-2, G6PDH-2, and 6PGD-2 have the highest average levels of H_T for individual taxa (not shown) and for pooled taxa. The mean value of H_T for all taxa over all loci is 0.33.

TABLE 2-24. Nei's genetic diversity statistics for individual and pooled taxa of *Petasites*. Included are gene diversity statistics for individual polymorphic loci for pooled taxa, and gene diversity statistics over all loci for individual and pooled taxa. H_T = total gene diversity; H_S = gene diversity within populations; D_{ST} = gene diversity between populations; G_{ST} = coefficient of gene differentiation.

LOCI	TAXON	H_T	H_S	D_{ST}	G_{ST}
6Pgd-2	ALL TAXA:	0.6644	0.4104	0.2540	0.3823
G6pdh-1		0.3798	0.0161	0.3637	0.9576
G6pdh-2		0.6752	0.1559	0.5193	0.7691
Lap-1		0.4700	0.0808	0.3892	0.8281
Lap-2		0.4549	0.0786	0.3763	0.8272
Adh-1		0.6171	0.2278	0.3893	0.6308
Adh-2		0.4684	0.1142	0.3542	0.7562
Skdh-1		0.4492	0.2366	0.2126	0.4733
Skdh-2		0.5525	0.3599	0.1926	0.3486
Pgi-2		0.7130	0.5701	0.1429	0.2004
Pgm-2		0.4604	0.4111	0.0493	0.1071
Pgm-3		0.4444	0.3890	0.0554	0.1246
ALL LOCI:	*P. frigidus* var. *frigidus*	0.3035	0.1770	0.1265	0.4168
	P. frigidus var. *palmatus*	0.3483	0.1486	0.1997	0.5732
	P. sagittatus	0.3183	0.1381	0.1801	0.5660
	P. X vitifolius	0.2533	0.1486	0.1047	0.4133
	ALL	0.3342	0.1606	0.1736	0.5196

Petasites X vitifolius has the lowest level of H_T with a value of 0.25, whereas var. *palmatus* has the highest level of H_T with a value of 0.35.

The average value of G_{ST} for var. *frigidus* and *Petasites X vitifolius* is 0.42 and 0.41, respectively. This indicates that most of the genetic diversity resides within (H_S) populations instead of among populations (D_{ST}), as is typical of outcrossing plants. In contrast, the average value of G_{ST} for var. *palmatus* and *P. sagittatus* is 0.57 and 0.57, respectively, indicating most the genetic diversity resides among populations (D_{ST}). The value of G_{ST} for all taxa (0.52) follows this trend.

Presented in Table 2-25 are genetic identities (*I*) and distances (*D*) for all pairwise comparisons of populations within four taxa of *Petasites*. The highest value of *I* (0.96) and lowest value of *D* (0.04) occurs between var. *palmatus* and *P. sagittatus*. The lowest value of *I* (0.87) and highest value of *D* (0.14) occurs between *P. X vitifolius* and *P. sagittatus*.

The mean and range of genetic identities and genetic distances for pair-wise comparisons of populations within each taxon of *Petasites* is presented in Table 2-26. The mean genetic identity values (and genetic distance values) in all taxa ranges from 0.74 to 0.88 (*D* = 0.32 to 0.13). The widest range of genetic identities, 0.49 to 0.98, and genetic distances, 0.02 to 0.72, occurs within var. *palmatus*. Conversely, the narrowest range of genetic identities, 0.82 to 0.99, and distances, 0.005 to 0.202, occurs within *P. X vitifolius*.

A cluster analysis derived from a matrix of genetic distances from pair-wise comparisons of populations of all taxa of *Petasites* is shown in Figure 2-35. The populations of different taxa do not form any large distinct clusters, but remain as an amorphous group.

TABLE 2-25. Mean genetic identities (upper triangle) and mean genetic distances (lower triangle) for all pair-wise comparisons of populations within four taxa of *Petasites*. Taxa are represented by first six letters of subspecific or specific epithet.

TAXON	FRIGID	PALMAT	SAGITT	VITIFO
Petasites frigidus var. *frigidus*	******	0.9484	0.9202	0.9258
Petasites frigidus var. *palmatus*	0.0530	******	0.9575	0.8836
Petasites sagittatus	0.0832	0.0434	******	0.8724
Petasites X vitifolius	0.0771	0.1238	0.1365	******

TABLE 2-26. Nei's mean genetic identities and mean genetic distances for four taxa of *Petasites*.

TAXON	MEAN GENETIC IDENTITY (RANGE)	MEAN GENETIC DISTANCE (RANGE)
P. frigidus var. *frigidus*	0.8348 (0.6387 - 0.9888)	0.1841 (0.0113 - 0.4484)
P. frigidus var. *palmatus*	0.7399 (0.4884 - 0.9760)	0.3187 (0.0243 - 0.7167)
P. sagittatus	0.7667 (0.5581 - 0.9938)	0.2745 (0.0062 - 0.5833)
P. X vitifolius	0.8774 (0.8171 - 0.9952)	0.1324 (0.0049 - 0.2020)

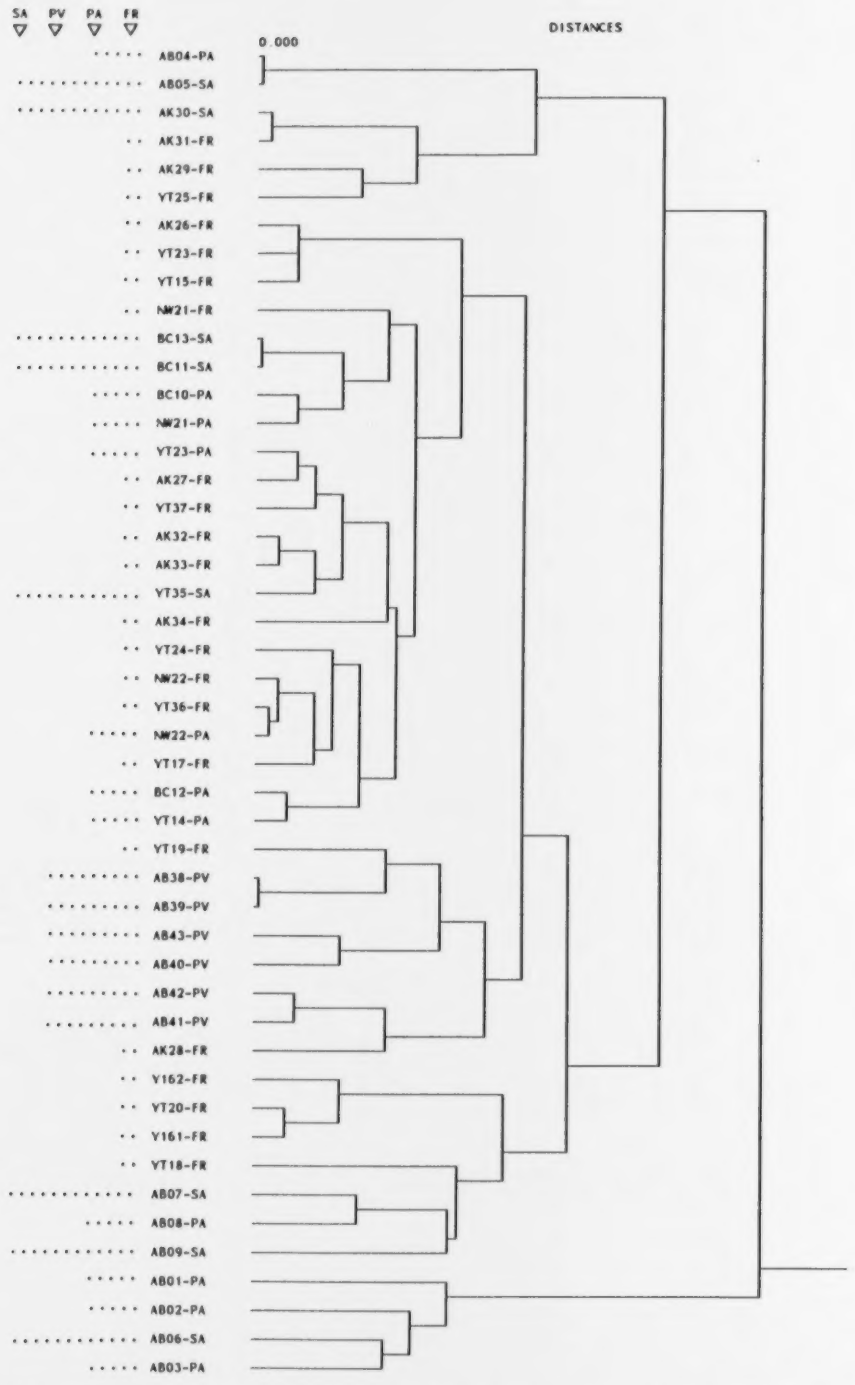

Figure 2-35. Average Linkage Tree Diagram derived from Nei's genetic distances of all pairwise comparisons of 47 populations of *Petasites*. Population designations consist of province/state, collection number, and taxon abbreviation: FR = *P. frigidus* var. *frigidus*, PA = *P. frigidus* var. *palmatus*, PV = *P. X vitifolius*, and SA = *P. sagittatus*.

DISCUSSION

Results from the cytological study, and morphometric and isozymic analyses are reviewed in order to assess the morphological variability and genetic diversity within and among populations and taxa of *Petasites*. Interpretations about the population genetic structure of *Petasites* are obtained from isozyme data. Based on information from all studies, the mode of speciation for taxa of *Petasites* in North America is inferred. The possibility of environmental conditions affecting the leaf form in *Petasites* is discussed in reference to results from previous studies of environmental influence on phenotypic plasticity. Additionally, interpretations of the relationships among the entities of the var. *frigidus* complex are presented and hypotheses for the origin of this group are discussed. The synthesis of information obtained from these studies provides the basis for the delimitation of the various taxa of *Petasites* in North America. The circumscription of these taxa is discussed and is in accordance with the species concept used in this study.

CYTOLOGICAL EVIDENCE

Petasites has thus far been considered as a diploid. However, Stace (1989) has suggested that *Petasites* is a hypohexaploid ($2n = 60 - 2 = 58$) that belongs to an ancient polyploid group that might have originated from one or several hybridization events. When considering that the proposed basic chromosome number of the Asteraceae is approximately $x = 9$ (Solbrig 1977) the likelihood of *Petasites* being a polyploid is not unreasonable.

The various authors who determined chromosome numbers in *Petasites* (Table 2-6) do not consider *Petasites* to be polyploid, but diploid, with approximately $2n = 60$ chromosomes. A few small chromosomes, which were thought to have resulted from fragmentation, were made accountable for the varying number of chromosomes (± 1 or 2) frequently observed in several species (Sørensen and Christiansen 1964). The basic chromosome number in *Petasites* was deduced to be $x = 29$ by Sørensen and Christiansen (1964).

Results from the enzyme analysis in this study support the supposition that *Petasites* is a diploid. Isozyme results for *Petasites* are most compatible with results for diploid individuals, not polyploids. *Antennaria* (Bayer 1987) has been considered to be an ancient polyploid which functions as a diploid. It is possible that a similar proposal may be applied to *Petasites*.

The individuals of var. *frigidus* from Barrow, Alaska that have been reported to have chromosome numbers of 90 provide evidence for the occurrence of polyploidy in *Petasites* (Packer and McPherson 1974). They are considered to be triploid autopolyploids. A triploid autopolyploid arises from the fertilization of a haploid gamete with an unreduced, diploid gamete.

Work with triploid populations of the homosporous fern, *Cystopteris protrusa*, has generated some interesting results which may be pertinent to the triploidy observed in *Petasites* (Haufler et al. 1985). Five triploid populations of *C. protrusa* from eastern North America were examined morphologically and isozymically. Prior work with this genus indicates that environmental conditions enhance meitotic irregularities and can promote the production of diploid spores. Haufler et al. (1985) suggested that the cold temperatures frequently experienced by *C. protrusa* may have prompted the formation of diploid spores in the five triploid populations. Furthermore, McHale (1983) has shown that similar conditions stimulate the production of diploid pollen in some angiosperms. Possibly, the cold fluctuations prevalent in Barrow also contributed to the formation of unreduced gametes.

Another proposal put forth by Haufler et al. (1985) is that triploidy may be an intermediate phase in the formation of fertile tetraploids. If diploid individuals are available to fertilize the sterile unreduced gametes of the triploids, a fertile tetraploid is formed. Evidence to support or reject this theory is not procurable from *Petasites* at this time.

It has been suggested that the increased heterozygosity, characteristic of polyploids, confers an adaptive ecological advantage which permits the occupation of new habitats (Haufler et al. 1984). Polyploids should be better able to adapt to new environmental conditions that the

diploids could not (Stebbins 1950). The occurrence of other diploid populations in Barrow, with no apparent differences in habitat (Packer and McPherson 1974), dismisses the possibility that the triploids are better able to survive in this region. There have been no other reports of polyploidy in *Petasites* taxa native to North America.

MORPHOLOGICAL ANALYSES

Systematists have attempted to delimit the various taxa of *Petasites* primarily on the basis of differences in leaf morphology. To determine if discrete groups could be recognized according to a combination of vegetative and/or reproductive characters, morphological data were subjected to principal components and discriminant analyses.

The morphometric analyses were initially executed with six taxa. After the unification of the three entities of the var. *frigidus* complex into one taxon, the analyses were again performed to observe the efficacy of such an amalgamation.

The principal components analyses have shown that all taxa of *Petasites* are only slightly separable in terms of the morphology of staminate and pistillate inflorescences (Figs. 2-19 to 2-22). The greatest separation of taxa occurred between the var. *frigidus* complex and var. *palmatus*. The differences in the characters which provided the greatest contribution to the variation in these taxa are predominately size related. *Petasites frigidus* var. *frigidus* tends to have fewer and more reduced values for characters than var. *palmatus*. It must be emphasized that var. *frigidus* plants as a whole tend to be of a smaller stature than some of the var. *palmatus* plants obtained from more southern localities. Since both vegetative and reproductive data were not obtained from the same individuals, correlations between leaf size and size of reproductive characters could not be demonstrated. However, such findings would substantially reduce the significance of some reproductive characters as taxonomic discriminators.

For both pistillate and staminate characters, *Petasites sagittatus* and *P. X vitifolius* overlap considerably. These taxa appear to occupy a morphologically intermediate position between var. *frigidus* and var. *palmatus* with respect to reproductive characters.

Although the leaves (Figs. 2-17, 2-18) show a much higher degree of separation between *Petasites sagittatus* and the other taxa, the morphological limits of these other taxa are not clearly defined. *Petasites frigidus* var. *palmatus* and *P. X vitifolius* are closely associated and form a group which is contiguous with the var. *frigidus* complex.

When the characters that provided the greatest contribution to the total variance were weighted, much better separation of taxa was achieved. This is evident in all of the discriminant analyses. However, after examination of the range of values for reproductive characters (Tables 2-8, 2-9), it is apparent that no strong discontinuities distinguish one taxon reliably from the other. The scatter diagrams (Figs. 2-23 to 2-24) tend to exaggerate the rather minuscule differences between taxa in order to achieve the degree of separation that is evident.

The possession of a mutually exclusive range of values or particular character state renders the most useful characters for taxonomic delimitation. Unfortunately, such provisions are limited in *Petasites*. Nevertheless, the extreme ends of some of the ranges do provide a certain degree of discriminating power for some taxa. An example is provided by the length of style branches for disc florets of staminate inflorescences (Table 2-8). A plant with a disc floret style branch length of over 2.00 mm can be reliably identified as *P. sagittatus*. Similarly, a plant with a style branch under 0.05 mm can be identified as var. *palmatus*. However, style branches intermediate between these extremes cannot reliably elucidate the identity of any particular taxon.

Results from the morphometric analyses demonstrate that the most reliable characters for delimiting the taxa of *Petasites* can be obtained from leaf morphology. *Petasites sagittatus* is, undoubtedly, the most morphologically distinct. The striking correct classification rate of 100% for leaf characters (Table 2-16) illustrates the cohesiveness of this group, attributed

principally to the low level of variability exhibited by the leaves. Only 4/215 (1.9%) members of *Petasites* have been misclassified as *P. sagittatus*. This demonstrates that leaf morphology of *P. sagittatus* is markedly discontinuous from the other taxa. The most discriminating characters responsible for this discontinuity are the lack of lobes and sinuses.

The scatter diagrams for leaf morphology (Figs. 2-17 and 2-18) show the var. *frigidus* complex to be a relatively cohesive group, whereas var. *palmatus* and *P. X vitifolius* overlap extensively to form a loose group contiguous with the var. *frigidus* complex. Inspection of minimum and maximum values for leaf characters (Table 2-7) reveals that there is a large proportion of overlap among these taxa, as occurs with the staminate and pistillate characters. Therefore, the reliability of leaf characters to discriminate among these taxa is notably diminished.

In theory, the use of as many vegetative and reproductive characters as possible at one time permits the most reliable taxonomic identification. In practice, however, it is common to find only reproductive inflorescences of *Petasites* plants before the leaves emerge. Thus, positive identification of *Petasites* to the varietal level is greatly impeded.

The greatly overlapping character values among the three entities of the var. *frigidus* complex in all morphological analyses is suggestive of a close relationship . The scatter diagrams of the centroids from the discriminant analyses clearly illustrate their close association. Together, they form a discrete group which exhibits some degree of discontinuity from all other taxa. On this basis, the unification of these three entities of the var. *frigidus* complex is supported.

ENZYME ANALYSIS

Genetic variation within and among populations and taxa of *Petasites* is assessed using allelic frequency data obtained from enzyme electrophoresis. This permits the understanding of the genetic structure within populations of *Petasites* and how its genetic structure compares with

other clonal species. The significance of the clonal nature of *Petasites* is discussed in reference to the amount of genetic diversity that its populations can maintain. On the basis of genetic similarity among taxa, the mode of speciation and time since speciation events occurred in *Petasites* is inferred. This has important implications for the interpretation of evolutionary relationships among the North American taxa of *Petasites*.

Genetic Variation Within Populations

Genetic variation within populations of all taxa in *Petasites* is markedly similar (Table 2-23). All populations exhibit comparable values for mean number of alleles per locus. The grand average of *A* for all 47 populations of *Petasites* is 1.54. The proportion of polymorphic loci exhibits large ranges in all taxa with an overall mean of 0.3833.

Hamrick and Godt (1989) compiled results from numerous studies of allozyme variation in plants with different life-history traits to summarize genetic variation in different plant groups. Allozyme diversity within populations of *Petasites* compares favorably with results from other taxa with similar life-history traits. The mean number of alleles per locus and proportion of polymorphic loci for dicots (1.44 and 0.29, respectively, Table 3; Hamrick and Godt 1989) was somewhat lower than what was demonstrated for *Petasites*. Results for long-lived herbaceous perennials (A = 1.44, P = 0.39) compared well with the overall mean of *Petasites* even though some individual populations had a mean that was somewhat higher and more comparable to woody perennials. The geographic range of a regional species (A = 1.55, P = 0.364) was also comparable to results for *Petasites*, although results from some populations were within the range for narrow and widespread species. Additionally, results for a temperate distribution (A = 1.51, P = 0.33) correspond with those of *Petasites*. Results from some populations indicated that *Petasites* was typical of a plant with an outcrossing-entomophilous breeding system (A = 1.54, P = 0.34) whereas other populations were more characteristic of mixed-animal species (A = 1.43, P = 0.29). Fruit dispersal for *Petasites* is effected by wind. Hamrick Godt's (1989)

results for this category are 1.70 for *A* and 0.43 for *P*. Although several populations of *Petasites* exhibited similar results for this category, overall results were more comparable to gravity (*A* = 1.45, *P* = 0.30) and gravity-attached (*A* = 1.64, *P* = 0.34) species. These findings coincide with the occurrence of seeds germinating while still attached to the capitulum (Bogle 1961). It is likely that those seeds that fell to the ground near their maternal parent would develop to maturity. An early (*A* = 1.46, *P* = 0.30) to mid (*A* = 1.52, *P* = 0.34) successional status compared favorably to *Petasites*.

Studies of other outcrossing, clonal, perennial species exhibit results that parallel those of *Petasites*. *Populus deltoides* exhibited a value of 1.59 for *A* and a value of 0.32 for *P* (Rajora 1989). Similarly, a study by Hughes and Richards (1988) demonstrated a value of 1.5 for *A* and 0.46 for *P* in diploid, outcrossing species of *Taraxacum*.

Mean values for observed heterozygosity, H_{obs}, for taxa of *Petasites* range markedly (0.09 to 0.19; Table 2-23). The mean H_{obs} for all taxa is 0.15, which is higher than the mean value of H_{obs} for populations of *Populus deltoides* (0.05; Rajora 1989). The mean value of H_{obs} for *Petasites* taxa compares favorably with diploid, outcrossing populations of *Taraxacum* (0.16; Hughes and Richards 1988), however.

The mean values of H_{obs} and H_{exp} for each taxon of *Petasites* do not differ significantly from each other (Table 2-23), although several populations within all taxa (22/47) exhibit significant differences. Deviations from Hardy-Weinberg equilibrium expectations can result from inbreeding, selection, mutation, and gene flow (Schaal 1975).

Heterogeneous environments commonly result in the subdivision of a population (Schaal 1975). This is largely due to the restriction of movement of pollen or seeds from which ensues inbreeding or the mating of closely related individuals. Schaal (1975) and Silander (1984) maintain that selection may be different in these subdivisions, therefore heterogeneity of allelic frequencies may reflect heterogeneity in the environment. It is possible that the high variability

observed in *Petasites* is the result of selection, and/or some other factor, operating differently on different loci in the various subpopulations.

Of the 27 populations of *Petasites* which deviate from Hardy-Weinberg equilibrium, nine populations have lower levels of heterozygosity than expected, indicating the occurrence of mating among closely related individuals. The remaining 13 populations exhibit higher levels of heterozygosity than are expected. Reasons for the results for these populations are discussed further in relation to their corresponding F_T values.

Values for the mean fixation index, F_T, (Table 2-23) are negative in 55% (26/47) of the populations. This indicates that outcrossing is occurring. Highly negative values of F_T occur because H_{obs} greatly exceeds H_{exp}. This is observed in four populations of var. *frigidus*: YT-920161, YT-920162, YT-92025, and AK-92032 and one population of var. *palmatus*: YT-92014. It is probable that gene flow from nearby populations has influenced the number of heterozygotes in these populations.

An excess of heterozygotes may also be the result of heterozygote advantage, which confers adaptive superiority. This supposes that heterozygotes are superior in fitness because recessive genetic defects are masked in the heterozygous state (Dobzhansky et al. 1977).

The positive values of F_T in the remaining 45% (21/47) of the populations (Table 2-23) is, presumably, the result of inbreeding effects (Hamrick and Godt 1989). Highly positive values of F_T are the result of a large deficiency of heterozygotes. This is evident in three populations of var. *palmatus*: AB-92002, AB-92004, AB-92008, and one population of *P. sagittatus*: AB-92009. These populations of var. *palmatus* were small and the absence of flowering inflorescences during early spring suggests they were strictly clonal. The individuals sampled were probably established from the same source and were closely related. This, in addition to an absence of gene flow would explain the observed increase in homozygotes than is typically observed in outcrossing populations.

As opposed to the small size of the populations of var. *palmatus*, the population of *P. sagittatus* that exhibited similar results was extremely large. Although the time of collection was past the seed stage, personal communication with one of the collectors indicated that this population had set seed earlier in the season and in the previous year. Clearly this was a sexual population. However, there were no nearby populations from which this population could obtain pollen for fertilization or seeds for its establishment. The extreme density of individuals in this population is additionally important. If these propagules were available the high density of individuals would likely have restricted their movement (Loveless and Hamrick 1984). Some effects of high density on pollinators includes reduced flight distance and flight directionality (Loveless and Hamrick 1984). Even seeds that might manage to germinate would have to overcome intense competition for resources. Possibly, the individuals that were sampled arose from seeds that were derived from mating with close relatives within the same population over several generations. This would contribute to the extremely high number of homozygotes that were observed. However, three isozymes with the potential for polymorphism were not scored in this population, due to poor resolution. With the addition of these data, the level of heterozygosity might have been elevated.

It must be emphasized that inbreeding alone cannot be responsible for the deviations from Hardy-Weinberg expectations in *Petasites*. If inbreeding was solely responsible, the deviations would be similar across all loci and consequently, the result would be a general deficiency in heterozygotes (Silander 1984). This was not observed in *Petasites*. It is most realistic to postulate that additional forces were also operating, differently affecting the different loci in the various subpopulations.

Genetic Diversity Among Populations

The average amount of genetic diversity (H_T) maintained among all populations of *Petasites* is 0.33 (Table 2-24). This value of H_T is comparable to other herbaceous long-lived

perennials (0.35) in addition to species with a widepread geographic range (0.35), and an early to mid successional status (0.33 and 0.29, respectively) (Table 4; Hamrick and Godt 1989). Interestingly, H_T in selfing species (0.33; Hamrick et al. 1989) is identical to that for *Petasites* (0.33). As previously mentioned, the crossing of closely related individuals produces effects comparable to inbreeding. In clonal populations this is a common occurrence. The differences in the results of the breeding system category in Hamrick and Godt's study (1989), however, were not considered to be significant.

The extremely low values of H_T for *Petasites X vitifolius* could be the product of examining too few populations from only a small segment of its geographic range. However, it is expected that a hybrid would possess a lower level of genetic diversity than is found in each of the parental species (Crawford 1990).

It is, perhaps, the clonal nature of *Petasites* which is the most salient feature which influences the amount of genetic diversity that its populations can maintain. Pleasants and Wendel (1989) discuss the advantages that asexual species have over sexual species in the preservation of genetic diversity in small populations. In sexual species, alleles can be lost by chance during sexual reproduction and by selection against individuals homozygous for rare alleles in the occurrence of inbreeding. Conversely, perennial asexual species may be less disposed to the loss of genetic variation because their capacity to live to an older age provides a greater time in which to pass on alleles (Pleasants and Wendel 1989). Cheliak and Dancik (1982) indicate that continued asexual reproduction in populations of the long-lived tree species, *Populus tremuloides*, results in the accumulation of a greater amount of variation than would occur in a sexually reproducing population.

However, the benefits of asexual reproduction are most fully exploited in combination with at least some degree of sexual reproduction. Many predominately asexual species alternatively reproduce sexually, thereby providing a continuous source of genetic variation (Pleasants and Wendel 1989). Cheliak and Dancik (1982) hypothesized that some Alberta

populations of *Populus tremuloides* have been asexually maintained for 8,000 to 10,000 years after their original establishment by sexual events. In *Petasites*, the presumed original establishment of populations from several different sexual propagules has provided an additional contribution to its relatively high values of genetic diversity. When compared to other clonal species it is shown that *Petasites* maintains a level of genetic diversity that is just slightly below that for species such as the dioecious, perennial *Populus tremuloides* (0.42; Cheliak and Dancik 1982), the grass *Spartina patens* (0.43; Silander 1984), and the lily species, *Erythronium albidum*, with both asexual and sexual modes of reproduction (0.42; Pleasants and Wendel 1989).

It is a matter of contention whether or not the high genetic diversity exhibited by many clonal populations of plants is correlated with niche differentiation. Several authors (Dobzhansky et al. 1977; Burdon 1980; Silander 1984) argue that the high genetic diversity is the result of diversifying selection. This supposes that natural selection favors genotypes that are associated with phenotypes well adapted to the environment (Dobzhansky et al. 1977).

Burdon (1980) observed considerable variation among different clones of *Trifolium repens* in an environment with a high degree of microsite heterogeneity. From this study, Burdon (1980) concluded that many factors in the environment, including competition, exert strong, disruptive selective forces on populations, and thereby propel individuals in different evolutionary directions. Such forces are responsible for the maintenance of the high genetic variability exhibited by many clonal populations.

Numerous other studies have not discovered any correlation between niche differention and particular genotypes in clonal populations (Ellstrand and Roose 1987). This was found to be the case for *Spartina patens* (Silander 1979). Silander (1979) emphasized that, in addition to environmental heterogeneity affecting the distribution of genetic variation, chance and historical effects may be influencial.

G_{ST}, the coefficient of gene differentiation, has an average value of 0.52 (Table 2-24) in *Petasites*. This indicates that 52% of genetic diversity resides among populations as opposed to within populations. This is reflected by a higher value for D_{ST} than for H_S.

The average G_{ST} value for *Petasites* is much higher than most values in Hamrick and Godt (1989) for other outcrossing, long-lived herbaceous perennials (0.21). In the category of breeding system, the G_{ST} value for selfing species, 0.51 closely parallels that of *Petasites* (Hamrick and Godt 1989). This high G_{ST} value is expected because it is characteristic of inbreeding populations to partition most of their genetic diversity among populations (Crawford 1990; Gottlieb 1981; Roberts 1983). As previously mentioned, clonal species such as *Petasites* possess a population structure that operates in a similar manner to selfing species. Therefore, they exhibit similar results.

Selfing species typically have greater differences among populations because different alleles may become fixed at several loci, whereas outcrossers tend to possess the same alleles, only in different frequencies (Crawford 1990). This, in combination with a lack of gene flow, contributes to the extreme differences that are often observed between populations of selfers.

It is expected then that the high divergence among populations of *Petasites* would result from the fixation of different alleles, as occurs in selfers. Inspection of allelic frequencies for each population (Appendix 7) shows that this is indeed the case. The frequencies of alleles at various loci varied considerably. Alleles in low frequency in some populations occurred in high frequency or were fixed in other populations. This commonly occurs in selfing species (Gottlieb 1981). A lack of gene flow between geographically distant populations provides a further contribution to the overall high proportion of genetic diversity that exists among populations.

Additionally, the fixation of alleles in *Petasites* may be the result of the colonization of populations from a few founder individuals which originated from a larger population. Colonizing individuals are endowed with only a limited proportion of the total genetic variation that was

present in the source population. This would promote the occurrence of genetic drift; and consequently, the fixation of different alleles in different populations.

The spatial structure of populations is also believed to play a role in the degree of differentiation exhibited between populations. According to Loveless and Hamrick (1984) and Heywood and Levin (1984) divergence is enhanced between populations with a linear distribution. Additionally, a patchy distribution affects pollinator behavior (Loveless and Hamrick 1984). Movement may be restricted within a patch and gaps between patches may serve as barriers to gene flow, thereby enhancing differentiation. Since the majority of populations of *Petasites* were distributed linearly along roadsides or in small patches, the effects of these spatial structures may have contributed to the high differentiation that is observed between populations.

Populations of var. *frigidus* and *Petasites X vitifolius* exhibit values of G_{ST} that are somewhat lower than the values of G_{ST} for the other taxa. This indicates greater genetic diversity within populations as opposed to among populations. This is more typical of outcrossing populations (Hamrick and Godt 1989; Crawford 1990). An explanation for this is that there may have been greater gene flow between some of these populations due to seed and pollen movement. The many neighboring populations of these two taxa lends support to this possibility. Additional support for the occurrence of outcrossing is derived from the negative values of F_T in the majority of the populations of these taxa (Table 2-23). The average value of H_S over all taxa of *Petasites* is 0.16. This is much lower than values of H_S in other long-lived, herbaceous perennials (0.28; Hamrick and Godt 1989) and is the consequence of the extremely high G_{ST} values.

Genetic Identities and Genetic Distances

Subspecific taxa usually exhibit high genetic identities similar to those for conspecific plant populations (above 0.90; Crawford 1990). However, there are exceptions. A genetic

identity value as low as 0.71 has been shown to occur in infraspecific taxa of the diploid shrub, *Solanum* (Whalen 1979). This is more characteristic of the average level of similarity that has been estimated for congeneric plant populations (*I* = 0.67; Gottlieb 1981). Similarly, the diploid perennial *Allium douglasii* (Alliaceae) exhibited genetic identity values of 0.72 between var. *douglasii* and var. *columbianum* and between var. *douglasii* and var. *constrictum* (Rieseberg et al. 1987). In another study by Crawford and Bayer (1981), a genetic identity value of 0.75 has been observed between interfertile varieties of *Coreopsis cyclocarpa* (Asteraceae), a diploid perennial. The genetic identity values for pair-wise comparisons between the various taxa of *Petasites* fall within this range (Table 2-25).

The highest *I* value between taxa of *Petasites* was found to occur between var. *palmatus* and *P. sagittatus* (*I* = 0.96). The lowest *I* values occurred between *P. X vitifolius* and *P. sagittatus* (*I* = 0.87) and *P. X vitifolius* and var. *palmatus* (*I* = 0.88). Although it was unexpected to find lower genetic identities between this hybrid and its parents, than between the hybrid and var. *frigidus* (*I* = 0.93), this *I* value is still comparible to other studies of hybrids. An example is provided by *Stephanomeria diagensis*, a diploid annual and hybrid product of *S. exigua* and *S. virgata*. It was found to have a genetic identity of 0.90 between its former parent and 0.81 between its latter parent (Gallez and Gottlieb 1982).

Since hybrids have been shown to exhibit additivity of alleles (Gallez and Gottlieb 1982; Crawford 1990) it might be expected that *P. X vitifolius* would possess alleles from both parents at particular loci. However, the individuals of *P. X vitifolius* that were electrophoretically examined did not show additivity of alleles. This situation only arises when the prerequisite of mutually exclusive alleles is met by the parental species. *Petasites sagittatus* and var. *palmatus* may not have diverged sufficiently at isozyme loci for this criterion to be fulfilled. Furthermore, if this condition did exist, additivity would only be representative of an F_1 generation. Such a situation might not be characteristic of a species with a hybrid origin. Instead the species might consist of different stabilized recombinant forms (Crawford 1990). Additionally, it cannot be

expected that additivity would occur at every locus. Therefore, many loci for many individuals from numerous populations must be examined before a hypothesis for hybrid speciation can be rejected (Crawford 1990). Although electrophoretic results do not lend support for a hybrid origin for *P. X vitifolius*, it has been verified through crossing studies performed by Bogle (1961).

The results for the parental taxa of *Petasites* and their hybrid derivative are most probably due to the numbers of populations electrophoretically assayed in *P. X vitifolius*, in addition to only 8 and 11 populations for var. *palmatus* and *P. sagittatus*, respectively. The monomorphism of two additional alleles (*6Pgd-2*^{d} and *Adh-1*^{c}) in all populations of *P. X vitifolius* undoubtedly contributed to the lower *I* values between this hybrid and its parents, than are normally found in outcrossers. Furthermore, the sharing of the low frequency allele, *Adh-2*^{d}, with only var. *frigidus* heightened the similarity that was measured between this latter variety and *P. X vitifolius* (I = 0.93; Table 2-25).

The mean and range of genetic identity values within each taxon of *Petasites* (Table 2-26) is lower and wider, respectively, than is generally found in other diploid, outcrossing perennials. Crawford and Smith (1984) observed the mean genetic identity within four varieties of *Coreopsis grandiflora*, herbaceous outcrossing perennials, to range between 0.89 to 0.99. Populations within *C. grandiflora* var. *harveyana* exhibited the widest range of *I* values, from 0.81 to 0.99 (Crawford and Smith 1984). The mean genetic identity within three Florida subspecies of *Helianthus debilis* ranged from 0.989 to 0.992 (Wain 1982). Genetic identity values between populations of *H. debilis* subsp. *debilis* ranged from 0.85 to 0.95.

Genetic identity values between populations of *Petasites* appear to be more comparable to selfing plants, which usually exhibit higher levels of genetic variation than outcrossers (Crawford 1990). McNeill and Jain (1983) performed an isozyme study on four species of *Limnanthes* (Limnanthaceae) with infraspecific taxa. The breeding system of these diploid annuals ranged from autogamous to almost completely outcrossing. *Limnanthes floccosa*

proved to be especially interesting. This species is comprised of five subspecies which have fully autogamous to partially outcrossing breeding system. It was found that the most autogamous subspecies, *L. floccosa* ssp. *floccosa*, had greater interpopulational differentiation than the more outcrossing taxa. The mean *I* value between pairwise comparisons of *L. floccosa* subspecies was 0.74 with a range from 0.58 to 0.99 (McNeill and Jain 1983).

Bidens discoidea provides another good example of a diploid, selfing annual which possesses a high level of genetic variation (Roberts 1983). Genetic identities between populations range from 0.69 to 0.99, with an overall mean of 0.87. Roberts (1983) suggests that these low levels of genetic diversity are probably the result of the randomness of dispersal and lack of gene flow between populations of different habitats. Additionally, there is a low correlation between *I* and geographical distance in *Bidens discoidea*, as occurs in Petasites.

The widest range of genetic identities, corresponding with the lowest mean, occurs within var. *palmatus* (Table 2-26). Inspection of the genetic variation for pairwise comparisons of populations of this taxon (Appendix 8) reveals that the lowest *I* value (0.49) and corresponding highest *D* value (0.72) occurs between two geographically distant populations, one from Alberta (AB-01PA) and one from the Yukon (YT-14PA). Such a high genetic divergence may reflect a lack of gene flow due to the geographical isolation between these two populations. However, another explanation may be, at least partially, due to the lack of allelic frequency data for four isozymes in AB-01PA and for two isozymes in YT-14PA. Resolution at these isozymes was inadequate, therefore the banding patterns were not interpretable. The highest value of *I* (0.98) and the lowest value of *D* (0.03) in var. *palmatus* occurs between a population in British Columbia (BC-12PA) and a population in the Yukon (YT-14PA) that are in relatively close geographical proximity. The high genetic similarity between these two populations may be the result of gene flow.

The phenogram derived from the cluster analysis of the genetic distance matrix permits the visualization of the associations among the 11 populations of var. *palmatus* (Fig. 2-35). The

largest genetic distance occurs between populations AB-01PA and YT-14PA whereas BC-12PA and YT-14PA are separated by the shortest genetic distance. The latter being an indication that these two populations are very similar isozymically.

The narrowest range of genetic identities (0.822 to 0.995) and genetic distances (0.005 to 0.202) occurs within populations of *Petasites X vitifolius*. Such a narrow range may reflect the close geographical proximity of the populations. They were all collected in the vicinity of Edmonton, Alberta. Additionally, only six populations of *P. X vitifolius* were examined, a small sample of the total variation that may be actually be present in this hybrid entity.

Within *Petasites X vitifolius* the highest value of *I* (0.995) and the lowest value of *D* (0.005) occurs between two populations that are the closest geographically, AB-38PV and AB-39PV (Appendix 8). The phenogram (Fig. 2-35) clearly shows their close relationship. The similarity between these two populations may reflect the homogenizing effect of gene flow from the movement of pollen and seeds. The lowest *I* value (0.817) and highest *D* value (0.202) occurs between two populations that are most geographically distant from each other, AB-38PV and AB-42PV (Appendix 8).

These correlations between geographical distance and values of *I* and *D* are not always consistent, however. Two relatively neighboring populations of var. *palmatus* from Alberta, AB-03PA and AB-04PA, exhibit an *I* value of only 0.72 and a *D* value of 0.33 (Appendix 8). These populations also form the most distant clusters in the phenogram (Fig. 2-35). Similar observations were also made in Robert's (1983) study of *Bidens discoidea*. Two populations from Connecticut that are separated by a distance of 25 km have a genetic identity of 0.688; whereas a Virginia population and a North Carolina population that are separated by 160 km have a genetic identity of 1.00 (Roberts 1983).

Furthermore, numerous reports have been published in which populations of different taxa of *Petasites* that are geographically close, are isozymically more similar than are some populations of the same taxon that are geographically more distant (Appendix 8 and Fig. 2-35).

The *I* value between two populations of different taxa from British Columbia (BC-10PA and BC-13SA) is 0.91 (*D* = 0.04), whereas it is 0.56 (*D* = 0.58) between two populations of the same taxon, one from Alberta and the other from Alaska (AB-09SA and AK-30SA). Gene flow cannot be used to explain the high genetic identity between the two populations of var. *palmatus* and *P. sagittatus*. If the genetic similarity between them was representative of gene flow, some sort of morphological intermediacy would be expected, none of which is evident in these morphologically discrete taxa. Similar conclusions were drawn by Bayer (1988) when he reported comparable results in a study of four species of *Antennaria* from western North America. Geographically neighboring populations of *Antennaria marginata* and *A. rosulata* are very different morphologically and ecologically but are very similar isozymically.

No cohesive clusters in the genetic distance phenogram (Fig. 2-35) are apparent. Although taxa are randomly grouped together there does appear to be some correlation between geographical proximity and genetic similarity. This study indicates that morphological divergence in *Petasites* is not associated with divergence at isozyme loci. Numerous other examples of plants exhibit similar results. One such study by Crawford and Ornduff (1989) examined genetic variation among three diploid, annual species of *Lasthenia* (Asteraceae) from California. Based on mean genetic identities of pair-wise comparisons of populations, the two most morphologically distinct species (*L. conjugens* and *L. fremontii*) were most similar isozymically; whereas, the two most morphologically similar species (*L. fremontii* and *L. burkei*) were the least similar isozymically.

Gottlieb (1984) has indicated that morphological differences are controlled by only one or a few genes. This makes it possible for speciation to occur without isozymic divergence; and conversely, for isozymic divergence to occur without speciation (Crawford 1985; Gottlieb 1981).

Speciation

Speciation events may be either rapid or gradual. Rapid speciation may lead to rapid differentiation in morphology, although it usually takes a longer period of time to accumulate allelic differences at isozyme loci. A rapid mode of speciation has been termed quantum speciation by Grant (1971). A slower, more gradual process of speciation would more likely result in changes at genes coding for isozymes, in addition to changes in morphology. Grant (1971) refers to this gradual process as geographical speciation.

Not only the kind of speciation that has occurred, but the amount of time since the speciation event, influences the amount of diversity that is present in a new species. Species that arose from a rapid speciation event that is recent may be morphologically different but have little divergence in isozymes. Many insular species have undergone a rapid adaptive radiation. Speciation has occurred very quickly and although the species may be extremely divergent in morphology, they are not at isozyme loci because there has not been sufficient time for the accumulation of genetic variation.

The three genera comprising the Hawaiian silversword alliance (Asteraceae) provide a classic example of adaptive radiation in an insular environment (Witter and Carr 1988). Members of these genera are found in virtually all habitats on the Hawaiian Islands and they exhibit a tremendous range of morphological variation. Despite the apparent morphological and ecological diversity in the alliance, however, interspecific genetic identities are high. The alliance is representative of plants which have undergone an adaptive radiation in a very short time after being founded on the Hawaiian Islands. Witter and Carr (1988) concluded that the time since speciation has not been sufficient for the accumulation of new genetic variation from mutations.

Lowrey and Crawford's (1985) allozyme study on seven species of *Tetramolopium* (Asteraceae) from the Hawaiian Islands yielded results that were comparable to the silversword alliance. Although these species are representative of three different sections and they exhibit distinctive differences in morphology and ecological preference, they have remained fully

interfertile. Furthermore, the high genetic identities exhibited between populations of different species and infraspecific taxa (0.87-1.00; Lowrey and Crawford 1985) are more suggestive of conspecific populations. The limited differentiation at genes coding for enzymes accompanied by the high morphological and ecological diversity in *Tetramolopium* has been interpreted to be the result of a rapid and recent divergence through an adaptive radiation into a myriad of habitats on the Hawaiian Islands.

When a long period of time has elapsed since a rapid speciation event, the species tend to have large differences in both isozymes and morphology, and less commonly in isozymes only. *Coreopsis cyclocarpa* (Asteraceae) provides an example where there is little divergence in morphology but high divergence in isozymes (Crawford and Bayer 1981). *Coreopsis cyclocarpa* consists of two diploid, perennial varieties which have disjunct distributions in Mexico. Although genetic identities were high within both species (0.95 and 0.98 for var. *pinnasecta* and var. *cyclocarpa*, respectively), a genetic identity of only 0.75 was observed between species. This low genetic identity value is believed to reflect the amount of time they had to accumulate genetic variation since they diverged (Crawford and Bayer 1981).

The relatively high values of genetic identities between the different taxa of *Petasites* and the similarity in isozymes and high frequency allozymes infers a rapid and recent origin in North America. It is interpreted that the taxa of *Petasites* are continueing to differentiate rapidly. The genetic similarity may be indicative of a previous, more continuous distribution of populations prior to the evolution of infraspecific taxa. The populations that are most divergent have likely been geographically separated for a longer period of time than other populations.

SUMMARY OF MORPHOLOGICAL AND ENZYMATIC ANALYSES

Evidence obtained from analyses of variability in morphology and enzymes indicates that North American *Petasites* is comprised of four similar and polymorphic entities. The enzyme analysis has shown that the distinction of separate taxa in *Petasites* could not be made using

information from isozymes. Although there are large interpopulation differences in allelic frequencies, these differences have no discriminatory value. There is indication of a weak, negative correlation between geographical distance and genetic identity, but this is also of little taxonomic significance. The relatively high genetic identities between all taxa is indicative of conspecific populations, and suggests a close relationship among the taxa.

Results from the enzyme analysis have proven useful in the understanding of the population genetic structure in *Petasites*. This study provides an additional contribution to the information available on clonal species. *Petasites* maintains a level of genetic diversity similar to other clonal species (Cheliak and Dancik 1982; Silander 1984). Additionally, *Petasites* exhibits high levels of genetic differentiation among populations. This is typical of selfing species and has also been observed in other clonal species (Silander 1984). This strong partitioning of genetic variation among populations in outcrossing species results from the mating of close relatives due to restricted movement of pollen and seeds.

Information about the mode of speciation and time since speciation occurred in *Petasites* has been obtained from the combination of results from both enzyme and morphological analyses. The high genetic identities between taxa of *Petasites* with the absence of many unique alleles, in addition to the similarity in reproductive morphology infers a rapid and recent origin of North American taxa of *Petasites*. The absence of correlations between divergence at isozyme loci and morphological features suggests there was insufficient time for the diverging taxa to accumulate mutations.

Morphological variation between different taxa of *Petasites* is continuous for most reproductive characters, therefore delimitation of taxa is difficult and impossible in many cases. *Petasites frigidus* var. *frigidus* and var. *palmatus* exhibit the highest degree of differentiation of all taxa of *Petasites*, although much of this is attributed to minute character differences.

Leaf characters of *Petasites* proved to be the most taxonomically discriminating. Many characters were overlapping across taxa, although some proved to be discontiuous and

therefore the most useful for successful taxonomic identification, particularly for *P. sagittatus*. Even though leaf characters have been shown to be the most taxonomically discriminating, this does not necessarily imply that the differences are genetically controlled. Factors responsible for the higher degree of divergence in the leaves of *Petasites* may be more environmental than genetic.

ENVIRONMENTAL INFLUENCE ON PHENOTYPIC PLASTICITY

The possibility that environmental conditions contribute to the high diversity in leaf form in *Petasites* must be addressed. Cutter (1971) explains that heterophylly, the occurrence of more than one leaf type in a species, results from differential activity of the various meristems involved in leaf development. Most often heterophylly is associated with changing environmental conditions or a particular developmental stage of the plant. The implications of this, in *Petasites,* is explored in the following discussion.

The processes operating between the environment and *Petasites* may be extremely complex. Light may play a role. Experimental evidence indicates that the length of photoperiod influences the degree of leaf dissection in aquatic and terresterial plants (Cutter 1971). It was shown that dissected and entire leaf types can develop on the same shoot (Cutter 1971). These differences in morphology depend on the amount and location of activity in the marginal meristems (Cutter 1971). More specifically, it was demonstrated that environmental factors can affect the degree of apical and marginal growth in the lobes of leaves.

A relationship between light and the degree of leaf dissection in *Petasites* may exist. Comparisons of leaves from plants collected in the field, with those grown from the same rhizome in the greenhouse verify such an influence. Plants grown in the greenhouse exhibited a reduction in leaf lobing, degree of dissection, and number of teeth. This was especially prominent in var. *palmatus*. These plants had been obtained from rather shady, forested

regions. The increased intensity of light may have influenced the variation in leaf form that was observed.

The possibility that extended periods of light reduce the degree of leaf dissection is suspected in *Petasites frigidus* var. *frigidus*. Lobed, entire leaves of the var. *frigidus* (*sens. strict.*) type occur in the high Arctic under a regime of 24 hours of daylight a day. The absence of the highly dissected and many lobed leaves of the var. *nivalis* type in the high arctic may indicate that prolonged periods of light reduce the degree of leaf dissection.

However, the influence of light on leaf dissection cannot explain the occurrence of both the var. *frigidus* and var. *nivalis* leaf types on one plant (refer to Fig. 2-10). This suggests that what is going on is much more complex than a simple linear relationship. Possibly, light may be only one of a combination of various factors involved.

Another environmental factor that may have an important influence on the leaf form in *Petasites* is temperature. In *Ranunculus flabellaris*, an aquatic species, submerged leaves are highly dissected whereas aerial leaves exhibit a more expanded blade with lobing. Cutter (1971) indicates that early development of shoot apices and leaf primordia are similar in both submerged and aerial shoot apices, and that low temperature induces the formation of dissected leaves on aerial shoots. Therefore, this environmental factor influenced the rate of formation of lobes in the developing leaves, affecting cell division directly.

The enigma of the plants with leaves of both the var. *frigidus* and var. *nivalis* leaf types can be best explained by the effects of temperature. The gently lobed form of the var. *frigidus* leaf type may be correlated with low temperature, characteristic of its alpine and arctic habitat. The highly dissected form of the var. *nivalis* leaf type may be diagnostic of higher temperatures. Possibily, a particular temperature was present for the emergence of the first leaf and a different temperature was present for the second leaf. Each distinct temperature could have influenced each leaf in a different way.

Numerous other environmental factors may contribute to the leaf variation observed in *Petasites*. Stebbins (1950) and Jones and Luchsinger (1986) discuss situations where differences in soil, nutrient, and moisture conditions influence morphology in various species.

In the absence of genetic evidence to account for the high diversity in leaf morphology of *Petasites*, it is tempting to interpret environmental factors to be the sole source of this variation. However, the influence of genetics in combination with environmental influence on the activity of various meristems cannot be excluded.

In *Tropaelum majus*, Cutter (1971) shows that leaf shape is controlled by two genes which affect differential cell division in early development. Different genotypes of various combinations of these genes produced leaf shapes that were either deeply lobed, shallowly lobed, or entire and lobeless. Although this pattern was established early in development, shape differences were not manifested until late in development.

Leaf morphology in the various taxa of *Petasites* maintains a certain degree of integrity. Within taxa, the variability in leaf morphology may be influenced by an environmental factor or a combination of factors, acting differently on different genotypes.

THE VAR. *FRIGIDUS* COMPLEX

This group of plants possessing highly variable leaf forms has proven to be taxonomically challenging. Various interpretations of the relationships within this group and its origin have been proposed. These are reviewed here and others are presented.

Hultén (1968) interprets the var. *frigidus* complex to represent two distinct species, *Petasites frigidus* and *P. hyperboreus* (= *P. frigidus* var. *nivalis* (Greene) Cronq.), which produce hybrid swarms in regions where their ranges are sympatric. He postulates that the numerous morphological intermediates have been generated from hybridization and introgression. Hultén considers *P. gracilis*, *P. alaskanus*, *P. arcticus*, and *P. frigidus* var. *hyperboreoides* to represent the three most common forms of intermediates that arise from the

hybrid swarms formed between these two species. Further proposed by Hultén is that *P. hyperboreus* Rydb.(= *P. frigidus* var. *nivalis* (Greene) Cronq.) is itself the product of hybridization between var. *frigidus* and var. *palmatus*.

Observations in the field, however, did not provide evidence to suggest that var. *frigidus* and var. *nivalis* exist as distinct entities. No populations were composed exclusively of these proposed "parental" forms, only combinations of all forms that occur in the complex. It is unlikely that every population consists of a hybrid swarm without the perpetuation of at least some pure parental populations, especially in very remote regions. On this basis, Hultén's hypothesis is rejected.

Nonetheless, a hybrid origin for this group is not dismissed. Possibly, the var. *frigidus* complex originated in the hybridization of two or more species with subsequent backcrossing and introgression. A reticulate pattern of evolution would certainly contribute to the high polymorphism which characterizes the var. *frigidus* complex. In contrast to Hultén, however, it is proposed that these hybridization events are historical, not current.

Backcrossing of the hybrids to the parental species would have resulted in the movement of genes from one taxon to the other by way of the hybrids themselves (Stebbins 1950). The morphological integrity of the parents would have then become obliterated over time. Therefore, as opposed to the opinion of Hultén, the progenitors of the var. *frigidus* complex may not be extant.

Another proposal to explain the derivation of the var. *frigidus* complex is that the leaf forms of var. *frigidus* (*sens. strict.*) and var. *nivalis* represent ecotypes adapted to two different habitats with intermediate forms occupying intermediate habitats. However, due to the ecological overlap of plants with the var. *frigidus* (*sens. strict.*) and var. *nivalis* leaf forms over much of their distributional range, which itself is overlapping, ecological differentiation is not evident. Moreover, the occurrence of both leaf forms has been observed on the same plant on

specimens in the field and on specimens in the herbarium. This largely dismisses the possibility of the leaf forms representing ecotypes.

Bogle (1961) posed an additional possibility. He suggested that at least some phase of *Petasites frigidus* var. *nivalis* could be the product of the gradual differentiation of a subalpine ecotype from var. *palmatus*. As previously mentioned, however, plants possessing both leaf forms of the var. *frigidus* and the var. *nivalis* type indicate they represent only one taxon.

Nevertheless, environmental influence on taxa of *Petasites* has not been excluded as has been previously discussed. It is plausible that temperature may be one environmental factor influencing leaf dissection. Such factors may directly influence the activity of various meristems in the leaf (Cutter 1971).

The occurrence of plants possessing leaves of the var. *frigidus* type (*sens. strict.*) and the var. *nivalis* type is certainly perplexing. At this stage in the research on *Petasites* it can only be concluded that these two leaf types, and the intermediate forms between them, are diagnostic of only one highly polymorphic taxon, *Petasites frigidus* var. *frigidus*. The favored hypothesis for the origin of the var. *frigidus* complex is the past hybrid origin and introgression of two or more taxa. The resultant derivatives could then have continued to evolve, further obliterating the morphological relationships to the parental species.

TAXONOMIC DELIMITATION

It is the decision to follow Cronquist's systematic treatment (1953), in part, and maintain *Petasites frigidus* var. *frigidus* and var. *palmatus* at the rank of variety. Although the circumscription of var. *palmatus* remains unaltered, the circumscription for var. *frigidus* has been revised. The circumscription of var. *frigidus* has been expanded to include the forms that Cronquist designated as var. *frigidus* and var. *nivalis* in addition to the forms that Hultén (1968) postulated to be the hybridized products of these two varieties (species; *fide* Hultén). It is also the decision to reduce *P. sagittatus* from the rank of species to varietal status under *P. frigidus*.

These latter two taxa are discussed separately in greater detail. *Petasites frigidus* var. *palmatus* and the stabilized hybrid, resulting from crosses between *P. sagittatus* and var. *palmatus*, are recognized *sensu* Bogle (1968) (Table 2-1). However, a new combination for the hybrid is proposed to accommodate the new status of *P. sagittatus* (Chapter 3).

The decision to include all North American taxa of *Petasites* in one species is in accordance with the species concept used (Cronquist 1978) in this study. The smallest groups criterion in this species definition is not met for the taxa of *Petasites* when considering reproductive morphology. If provided with individual inflorescences without associated leaves, they could be readily distinguished as *Petasites*, but it would be difficult to recognize less inclusive groups. Therefore, the smallest group would be the species *Petasites frigidus*.

On the basis of this premise, the species criterion for consistency cannot be fulfilled using reproductive morphology. Although extreme values for certain characters are specific to some taxa, none of these taxa can be reliably and consistently identified with the use of reproductive characters alone. Variation between the groups is not discontinuous, therefore, individuals do not clearly belong to one group and not the other.

The species criterion for persistency is also unsatisfied in *Petasites*. Due to the absence of reproductive barriers, hybridization commonly occurs among all taxa of *Petasites*. Consequently, phenetic discontinuity is not persistent among the different groups.

On the basis of vegetative morphology, there is enough variation in *Petasites* for further subdivision into taxonomic groups, therefore, these taxa could reasonably be considered to be the smallest groups. However, the discontinuity in variation between these groups is too slight to prevent misidentification. Consequently, the consistency criterion is not met. As for reproductive morphology, the persistency criterion is not fulfilled with leaf morphology due to hybridization among all taxa. Therefore it is also concluded that, on the basis of leaf morphology, discontinuity between groups is insufficient to warrant their recognition at the rank of species.

Petasites sagittatus exhibits the most cohesive vegetative morphology, largely due to the low level of variability expressed in the leaves. On the basis of morphological distinction of the leaves, it might be argued that *P. sagittatus* should remain at the rank of species. Members of this group cannot be further divided into smaller groups, thereby meeting the smallest groups species criterion. Leaf morphology of *P. sagittatus* also exhibits the highest discontinuity with the other groups. Hence, for this taxon, the species criterion for consistency is also fulfilled. However, the ability to hybridize with all other taxa prevents *P. sagittatus* from meeting the requirement for persistency.

Moreover, all morphological characters must be considered. The pistillate morphology of *P. sagittatus* received the lowest rates of correct classification (Table 2-22) indicating a slight discontinuity with the other taxa. Additionally, the low levels of variability in pistillate and staminate characters for all taxa and the lack of reproductive barriers suggests that they are all closely related. Variation in *P. sagittatus* is not sufficiently discontinuous in all morphological features to meet the species criterion of consistency. For these reasons, in combination with the close isozymic relationship of *P. sagittatus* with the other taxa of *Petasites*, this taxon is ranked as a variety as the other members of *Petasites* have been.

The entities which comprise the var. *frigidus* complex exhibit widely overlapping ranges in all morphological attributes. Consequently, each entity is not considered to be *consistently distinct*, as is evident by the rates of misclassification in Tables 2-16, 2-19, and 2-22. As a group, however, the var. *frigidus* complex does maintain a certain degree of integrity which sets it apart from the other taxa. Therefore, it is suggested that the entities in this group be united and recognized under one taxon.

The var. *frigidus* complex is not considered to be sufficiently differentiated, morphologically or isozymically, from the other taxa to warrant the designation of the rank of species. Alternatively, this complex is best treated as the highly polymorphic typical variety of *Petasites frigidus*. It is proposed that this complex be united under *P. frigidus* var. *frigidus*.

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CHAPTER THREE

A TAXONOMIC REVISION OF NORTH AMERICAN *PETASITES*

INTRODUCTION

North American *Petasites* Mill. is a genus of perennial rhizomatous herbs widely distributed across Canada, Alaska, and the northern contiguous United States. This genus is taxonomically difficult as a result of a highly conservative floral structure accompanied by a highly diverse leaf form. Between several extreme leaf forms are numerous intergrading forms, all of which have been reported to be interfertile (Bogle 1961). The absence of marked discontinuities between these leaf forms of the various taxa of *Petasites* has generated considerable confusion surrounding the taxonomic delineation of the genus.

Traditionally, taxonomists have constructed classification systems of *Petasites* based on slight differences in leaf morphology. Since the precise relationships among the various taxa in *Petasites* have not been explicitly defined, however, it has not been clear how much polymorphism in the leaves is inherent within each taxon, and how much of it might be attributed to environmental influence or hybridization.

The taxonomic ambiguity in *Petasites* is reflected in the inconsistencies of the various circumscriptions of the species. Rydberg (1927) recognized as many as ten species native to North America, whereas Cronquist (1953) recognized only two species: *P. frigidus* with three varieties and *P. sagittatus*. Cronquist considered *P. sagittatus* to be morphologically differentiated enough to warrant species recognition. Bogle (1968) agreed with Cronquist's (1953) system for the most part, but posed the possibility that *P. sagittatus* might be conspecific with *P. frigidus*. This suggestion was not unprecedented, however, as Hooker (1833) recognized that all taxa of *Petasites* were distinguished by only minute differences and suspected that they all might belong to only one species.

A notable contribution to the understanding of relationships in *Petasites* was provided by Bogle with the elucidation of the hybrid origin of *P. vitifolius* in 1961. He later modified Cronquist's (1953) system by removing this hybrid from synonomy with var. *nivalis* and designating it as the binomial *P. X vitifolius* (Bogle 1968).

A center of controversy in *Petasites* is the status of the entities that have been collectively designated as the var. *frigidus* complex. This includes *P. frigidus* var. *frigidus*, var. *nivalis*, and forms intermediate in morphology between these taxa. Hultèn (1950) treated these intermediates as hybrid products of var. *frigidus* and var. *nivalis* (= *P. hyperboreus* Rydb.). Bogle (1961) was supportive of this hypothesis. Further contributions to the classification of *Petasites* are discussed in greater detail under the Taxonomic Treatment heading.

The inability of authors to agree on the relationships and subsequent taxonomic boundaries in *Petasites* has resulted in the production of ambiguous keys which do not discriminate among taxa. New characters, in addition to those from leaf morphology, must be selected to improve the effectiveness of keys to reliably distinguish taxa.

In order to resolve the taxonomic ambiguity in *Petasites* it is necessary to elucidate the phenetic and evolutionary relationships among the various taxa. This was accomplished in Chapter Two. In this chapter, the objectives are to present these relationships and to construct a key to aid in the correct identification of specimens. Additionally, a taxonomic treatment including a list of nomenclatural and taxonomic synonyms with their taxonomic history is provided.

RELATIONSHIPS

The interpretation of the relationships among the various taxa of *Petasites* has been determined with the use of morphological, isozymic, and chromosomal data in addition to direct observation of herbarium and field specimens (Chapter Two). Morphological data were subjected to principal components analyses and discriminant analyses to determine phenetic

relationships. An analysis of isozyme variability was undertaken to provide an assessment of the genetic divergence between the different taxa. Chromosome numbers were determined to provide further information on relationships within *Petasites*.

Morphological divergence in *Petasites* is not associated with divergence at isozyme locl. Although extreme differentiation was exhibited between some populations, this was due to differences in frequencies of the most common alleles as opposed to the possession of unique alleles. Therefore, differences at isozyme loci are not taxonomically significant in *Petasites*.

The similarity in isozymes suggests a close relationship among the different taxa, however, and is indicative of a relatively rapid and recent evolution. Although there has been sufficient time for a certain degree of morphological divergence, it is considered insufficient for the accumulation of large numbers of unique features. All taxa of *Petasites* possess the same chromosome number, approximately $2n = 60$. This further supports a close relationship of taxa in *Petasites*.

Morphometric analyses have demonstrated that taxa of *Petasites* cannot be delimited with the use of reproductive characters alone. Staminate and pistillate characters are continuous with a high degree of overlap between taxa. This notably diminishes their discriminating power. It should be noted, however that the extreme ends of variation in some characters proved to be taxonomically discriminating for some taxa. Leaf morphology provides the best characters with which to discriminate taxa of *Petasites*. Although many character values overlap between taxa, several are useful in taxonomic delimitation. The leaf form of *P. sagittatus* emerged as the most distinct.

TAXONOMIC DELIMITATION

Based on the similarity in isozymes and chromosome number, in addition to the close association of morphological features, North American *Petasites* is interpreted as one

polymorphic species with infraspecific taxa. It is the decision to follow Bogle's (1968) circumscription of *Petasites*, in part. The circumscription of var. *palmatus* is maintained in the sense of Bogle (1968). Although the circumscription of *P. sagittatus* and *P. X vitifolius* remains the same as that of Bogle (1968), new combinations are proposed. Additionally, the circumscription of var. *frigidus* has been revised.

Although *Petasites sagittatus* exhibits marked differentiation in terms of leaf morphology, this is based primarily on three characters. Reproductive morphology and isozymes are not differentiated sufficiently in *P. sagittatus* to warrant recognition at the specific rank. Therefore, *P. sagittatus* is ranked as a variety of *P. frigidus*.

Since the status of *Petasites sagittatus* has been modified so must the name for the hybrid between this taxon and var. *palmatus*. Therefore, the new name *P. frigidus* var. *X vitifolius* is proposed.

It is further proposed that the entities comprising the var. *frigidus* complex be united under one taxon. Support for this unification comes from the morphological analyses. The entities, as a whole, maintain a certain degree of morphological integrity while remaining somewhat distinct from the other taxa. The possession of both var. *frigidus* and var. *nivalis* leaf forms on the same plants provides additional support for the interpretation of these entities belonging to one highly polymorphic group (Fig. 2-10). Moreover, experimental studies of environmental influence on leaf morphology in other species (Cutter 1971) suggests a similar possibility for the var. *frigidus* and var. *nivalis* leaf forms in *Petasites*. It is suspected that light and\or temperature are important factors affecting leaf dissection in *Petasites*. The extremely high degree of polymorphism in this variety may also be, in part, the consequence of a multiple hybrid origin. The var. *frigidus* complex is not sufficiently differentiated, morphologically or isozymically, from the other taxa to warrant the designation of the rank of species. Therefore, the formerly recognized var. *nivalis* (Greene) Cronq., in addition to intermediates considered to be hybrids by Hultén (1950), are united as the polymorphic typical variety *P. frigidus*. It is duly

noted, that hybridization freely occurs between all taxa, further enhancing the morphological diversity in *Petasites* and obscuring taxonomic boundaries.

The synthesis of the abovementioned studies indicates that these taxa of *Petasites* are closely related. The similarity in isozymes and reproductive morphology suggests a rapid and recent origin of North American taxa. This group is considered to still be in a rapid process of speciation. Taxa of North American *Petasites* have not yet reached a level of differentiation in morphology or isozymes which is indicative of distinct species.

Morphological Characters

With the utilization of principal components analyses, discriminant analyses, and examination of field and herbarium specimens, characters which contribute to most of the total variation have been determined (Chapter Two). These characters provide the best discrimination between taxa of *Petasites* and have been used in the construction of a key. Characters obtained from leaf morphology include the number of primary lobes, depth of sinuses, and number of teeth. The most discriminating staminate characters are number of heads, number of ray florets, style texture of disc florets, and length of style branches of disc florets. From pistillate morphology the most meaningful characters for taxonomic discrimination include number of heads, length of style branches of disc florets, phyllary margin, and disc corolla lobe length.

TAXONOMIC TREATMENT

Perennial herbs with thick creeping rhizomes; *basal leaves* with long petioles, blades sagittate, deltoid, cordate, reniform, or orbicular with entire to dentate and shallowly to deeply dissected margins, lobe shape obtuse to acute, adaxial surfaces glabrous to extremely woolly, becoming glabrate with age; *flowering stalks* arising from rhizome in early spring, usually prior to basal leaves, 1-10 dm high; *cauline leaves* on flowering stalks, alternate, reduced to parallel-veined, sessile or ensheathing bracts with inflated lamina at tip with shape characteristic of

vegetative foliage; *heads* several to numerous, gynodioecious, racemose or corymbose; *involucre* a series of bracts, generally in one series, often with a few shorter outer bracts, often purplish; *receptacle* flat, naked; *pappus* of numerous white capillary bristles; *staminate heads* consisting of numerous perfect disc florets, functionally staminate, corolla whitish, 5-cleft, styles branches lanceolate with long sweeping hairs, apical appendage of anthers rounded to triangular, disc florets surrounded by a row of sterile, pistillate ray florets, whitish, style undivided to clavate, surface papillose; *pistillate heads* comprised of numerous fertile pistillate ray florets, whitish or tinged red, ray florets exhibit a reduction in length of the ray from the periphery to the center where corolla becomes filiform, style undivided to clavate, surface papillose, a few perfect, sterile disc florets in center of head with 5-cleft corolla, styles branches lanceolate with long sweeping hairs, apical appendage of anthers rounded to triangluar; *achenes* linear, 5 to 10 nerved, glabrous, rarely villous, beakless elongating in fruit; chromosome number x = 29.

Petasites is commonly found in disturbed habitats and moist woods. It is also representative of alpine and subalpine slopes, fens, bogs, meadows, lake shores, stream banks, in addition to dry sites such as gravelly slopes and roadsides. The distribution of this genus is circumpolar. Its range extends from North Africa and western Europe eastward to northern and central North America. Within North America, *Petasites* is distributed across Canada, Alaska, and the northern contiguous United States extending as far south as California.

Key to North American varieties of *Petasites frigidus* (L.) Fries

1A. *Leaves* sagittate, deltoid, or cordate, not reniform or orbicular, margins entire to wavy to dentate with as many as 60 teeth, not lobed, adaxial surface glabrous to tomentose, abaxial surface villous to extremely woolly; *staminate heads* 8-35, style branch length of disc florets 0.50-3.20 mm, style texture of disc florets hairy, ray length 1.0-7.7 mm; *pistillate heads* 6-34, style texture of disc florets hairy, ray florets 31-139, ray length 0.6-5.4 mm, pappus length of ray florets as long as 17.3 mm, disc corolla lobe length 0.4-1.8 mm . . . . . *Petasites frigidus* var. *sagittatus*

1B. *Leaves* sagittate, deltoid, cordate, reniform, or orbicular, margins distinctly lobed or dentate only with not more than 22 teeth, if dentate only, adaxial surface mostly glabrous or sparsely tomentose, abaxial surface floccose, if lobed, adaxial and abaxial surfaces glabrous to woolly; *staminate heads* 2-32, style branch length of disc florets 0-2 mm, style texture of disc florets papillose to hairy, rays absent or present, if present as long as 12 mm; *pistillate heads* 5-42, style texture of disc florets papillose to hairy, ray florets 1-70, rays absent or present, if present as long as 6.3 mm, pappus length of ray florets as long as 15 mm, disc corolla lobe length 0.4-4.4 mm 2

2A. *Leaves* orbicular, deeply cordate to reniform, palmately lobed with 5-11 primary lobes, lobes may be cleft almost to center, 0-13 secondary lobes, margins entire to dentate with as many as 52 teeth; *staminate heads* 8-42, style branch length of disc florets 0-1.7 mm, ray florets 5-70, rays absent or present, if present as long as 6.3 mm; *pistillate heads* 4-32, ray florets 51-125, rays absent or present, if present as long as 6.3 mm, pappus length of ray florets as long as 11.8 mm, disc corolla lobe length 0.5-2.9 mm . . . . . *Petasites frigidus* var. *palmatus*

2B. *Leaves* sagittate, deltoid, reniform, or cordate, margins distinctly lobed or dentate only, if lobed, as many as 14 primary lobes and 0-25 secondary lobes, if dentate only, as many as 22 teeth, if lobed as many as 44 teeth; *staminate heads* 2-32, style branch length of disc florets 0.05-2 mm, ray florets 1-27, ray length 1.6-12 mm; *pistillate heads* 5-34, ray florets 30-109, ray length 0.8-4.8 mm, pappus length of ray florets as long as 15 mm, disc corolla lobe length 0.4-4.4 mm 3

3A. *Leaves* deltoid or mostly cordate, edges at base convex-curved, 4-14 shallow triangular primary lobes, 0-11 secondary lobes, lobes entire to dentate with as many as 44 teeth; *staminate heads* 3-32, style branch length of disc florets 0.4-1.4 mm, ray florets 2-27, ray length 2.1- 7.8 mm; *pistillate heads* 9-34, ray florets 48-89, ray length 0.8-2. mm, pappus length of ray florets as long as 7 mm, disc corolla lobe length 0.8-2.0 mm . . . . . *Petasites frigidus* var. *X vitifolius*

3B. *Leaves* sagittate, deltoid, or reniform to cordate, margin lobed or dentate only, if dentate only, as many as 22 teeth present, if lobed as many as 14 primary lobes, entire or dentate, 0-25 secondary entire or irregularly toothed lobes, shallowly lobed or deeply parted, in extreme forms lobes with at least 2 lateral triangular teeth, lobes often overlapping, sinuses oblong and closed; *staminate heads* 2-20, style branch length 0.05-2 mm, ray florets 1-13, ray length 1.6-12 mm; *pistillate heads* 5-19, ray florets 30-109, ray length 0.8-4.8 mm, pappus length of ray florets as long as 15 mm, disc corolla lobe length 0.36-4.4 mm . . . . . *Petasites frigidus* var. *frigidus*

Ennumeration of Taxa

Petasites ***frigidus*** (L.) Fries var. ***frigidus***, Leaflets of Western Botany VII 30. 1953.

Tussilago frigida L., Sp. Pl. 865. 1753. *Nardosmia frigida* (L.) Hook. Fl. Bor. Am. 1: 307. 1833. *Petasites frigidus* (L.) Fries, Summa Veg. Scand. I: 182. 1845. *Nardosmia angulosa* Cass., Dict. Sci. Nat. 188. 1825; nom. illegit. *Nardosmia frigida* var. *genuina* Herder, Bull. Soc. Nat. Mosc.: 372. 1865. *Petasites frigidus* var. *genuinus* Cronq., Rhodora 48: 123. 1946. *Petasites frigidus* subsp. *frigidus* Folia Geobot. Phytotax. Praha 7: 389. 1972. TYPE: Lapland. (HOLOTYPE: photo LINN-995.17!).

Tussilago corymbosa R. Br., Chloris Melv. 21-22. 1823. *Nardosmia corymbosa* (R. Br.) Hook., Fl. Bor. Am. 1: 307. 1833. *Nardosmia frigida* var. *corymbosa* (R. Br.) Herder, Bull. Soc. Nat. Mosc. 38: 372. 1865. *Petasites corymbosus* (R. Br.) Rydb., Bull. Torr. Bot. Club. 37: 460. 1910. *Petasites frigidus* var. *corymbosus auct. non* R. Br.: Cronq., Rhodora 48: 123. 1946. TYPE: "Parry's First Voyage 1819. `Melville Island' the probable locality, but Baffin Land [was] (Hopper Land and E. coast) visited" (fide label), *Capt. Sabine 407* (LECTOTYPE-designated here: BM-000203!).

Petasites nivalis Greene, Pittonia II: 18-19. 1889. *Petasites frigidus* var. *nivalis* (Greene) Cronq., Leaflets of Western Botany VII: 30. 1953. *Petasites nivalis* subsp. *nivalis* Toman, Folia Geobot. Phytotax. Praha 7: 390. 1972. TYPE: "Washington, Mt. Ranier" (fide label), Aug. 21, 1889, *Edw. L. Greene s.n.* (LECTOTYPE-designated here: NDG-062357!; ISOLECTOTYPE: NDG-062358!).

Petasites gracilis Britt., Bull. NY. Bot. Gard. 2: 186. 1901. TYPE: "Walker Gulch" (fide label), July 16, 1899, *R.S. Williams s.n.* (HOLOTYPE: NY!).

Petasites alaskanus Rydb., N. Am. Fl. 34: 314. 1927. TYPE: "St. Paul's Island, Alaska" (fide label), 1879, *Dr. Robert White s.n.* (HOLOTYPE: NY!).

Petasites hyperboreus Rydb., N. Am. Fl. 34: 312-313. 1927. *Petasites nivalis* subsp. *hyperboreus* (Rydb.) Toman, Folia Geobot. Phytotax. Praha 7: 390. 1972. TYPE: "Second summit W. of Skagit River, B.C." (fide label), July 22, 1905, *J.M. Macoun Canad. Geo. Survey #76977* (HOLOTYPE: NY! Type description reads "76944" *not* "76977"; ISOTYPE: CAN-108732!).

Petasites frigidus var. *hyperboreoides* Hultén, Fl. Aleutian Isl. 328. 1937. LECTOTYPE: False Pass Unimak I, *Eyerdam 1798* (H).

TYPE MATERIAL AND NOTES ABOUT SYNONOMY

Petasites frigidus (L.) Fries var. *frigidus* was originally described by Linnaeus as *Tussilago frigida* in Species Plantarum (Linnaeus 1753). Linnaeus took the diagnosis for *T. frigida* from his earlier work, Flora Lapponica of 1737, along with four synonyms.

Since it was not possible to obtain the actual Linnaean type specimen, a photograph of the type material was examined. Specimen 995.17 LINN has been determined to be the holotype. Written on the herbarium sheet is "303", a reference to the collection numbering system from Linnaeus' Lapland herbarium. This number is also cited in Linnaeus' description of *T. frigida* in Species Plantarum (1753), authenticating the associated specimen's status as an original element. Savage (1945) has verified that the writings on the herbarium sheet have been written by Linnaeus (Fig. 3-1).

Figure 3-1. Holotype of *Tussilago frigida* L. (BM). Bar = 4 cm.

995.7

303

f. fragida

Linnaeus' Lapland herbarium is now located at the Library of the Institut of France, Paris. It has been determined that it contains a sheet consisting of a single fruiting capitulum and a single leaf which is associated with the publication of *T. frigida* L. (C.E. Jarvis (BM), pers. corresp.). It is believed that the sheet 995.17 LINN, from the Linnaean Herbarium in Picadilly, is a duplicate of this collection. However, it was not possible to obtain the specimen from Paris. These two specimens, in addition to 995.14 LINN, a specimen in Herb. Burser X: 154 (UPS), and at least two illustrations are original elements for Linnaeus' name (C.E. Jarvis (BM), pers. corresp.). These latter four elements are considered to be isotypes.

Inspection of photographs of the original specimens provides an insight into Linnaeus' concept of this taxon. The specimen from UPS is merely toothed, whereas 995.17 LINN is gently lobed, and 995.14 LINN is irregularly and coarsely lobed and toothed. This latter specimen, included in *Tussilago frigida* by Linnaeus, resembles the form that Hultén regarded as a hybrid between *Petasites frigidus* L. Fries and *P. hyperboreus* Rydb. *sens. strict.*

Cassini (1865) included *Tussilago frigida* in the segregate genus *Nardosmia* as *N. angulosa*. This is a superfluous name and is therefore illegitimate. The Linnaean epithet *frigida* had precedence over *angulosa*. In 1833, Hooker made the correct combination *N. frigida*. Although Hooker (1833) chose to maintain this taxon at the specific rank, he noted its similarity with the other North American species of the genus. He acknowledged the possibility that these taxa might constitute only one species. Fries (1845) later transferred *Nardosmia* to *Petasites*. Herder, however, chose to continue to recognize this taxon as *Nardosmia*. In 1865, Herder accomplished what Hooker had only alluded to, although he preferred to maintain two species instead of one. He reduced four species of *Nardosmia* to varietal status under *N. frigida*. According to Herder the variety *genuina* represented the genuine form of *N. frigida*. Although Cronquist (1946) agreed with Herder's circumscription, he preferred to recognize the genus as *Petasites* as Fries had done. He made the transfer forming *P. frigidus* var. *genuinus*.

In compliance with the International Code of Botanical Nomenclature (ICBN) rules for the automatic establishment of autonyms in the naming of infraspecific taxa, Cronquist changed *Petasites frigidus* var. *genuinus* to var. *frigidus* in 1953. Toman's interpretation of *P. frigidus* included only two infraspecific taxa, however, one circumpolar and one European. He chose to recognize them at the subspecific level. The name *P. frigidus* subsp. *frigidus* represented the circumpolar entity (Toman 1972).

Tussilago corymbosa, a taxon based on a plant collected from Parry's First Voyage on Melville Island, was described by Robert Brown in 1823. According to Brown, it differed from *T. frigida* in having numerous flower clusters and leaves that were "*minus alt sinuatis*" (less highly wavy). Cronquist (1955) indicates that the type is a specimen collected by Sabine on Melville Island. In contrast, Hultén (1950) suggests that the type consists of a single leaf collected by James Ross. Three specimens of *T. corymbosa* from Capt. Parry's voyage have been examined. The one specimen, collected by Sabine, that most closely fits Brown's description is one in which the leaf lobes are themselves toothed.

Hooker proposed the new combination *Nardosmia corymbosa* in 1833. Herder (1865) later reduced *N. corymbosa* to varietal status under *N. frigida*. Rydberg transferred *N. corymbosa* to *Petasites* in 1927. He maintained that this taxon was distinct from *P. frigidus* and preferred to recognize it at the specific rank.

Cronquist (1946) followed Herder (1865) and included *Petasites corymbosa* in *P. frigidus* as a variety. His interpretation of this taxon was based on a specimen which was later questioned by Fernald (Cronquist 1946) and Hultén (1950). Apparently, Cronquist had not examined original material used by Brown. According to Hultén, Cronquist's var. *corymbosa* was more representative of *P. hyperboreus* Rydb. than *P. corymbosus* (R. Br.) Rydb. After examining actual material of *Tussilago corymbosa*, Cronquist (1953) agreed with Hultén and Fernald that he had made an error. *Petasites frigidus* var. *corymbosus* as Cronquist understood it, was *auct. non*, "not in the sense" of Robert Brown. Noting the similarity between Brown's

type and *P. frigidus*, he placed *T. corymbosa* in synonymy under *P. frigidus* var. *frigidus*. He also noted the similarity between the entity in question and *P. nivalis* Greene (= *P. hyperboreus* Rydb.). He renamed the entity he had referred to as *P. frigidus* var. *corymbosa*, *P. frigidus* (L.) Fries var. *nivalis* (Greene) Cronq.

With *Petasites frigidus* var. *nivalis*, Cronquist also included *P. trigonophylla* Greene, and *P. vitifolius* Greene. In 1968, Bogle removed these latter two taxa from var. *nivalis* and proposed the binomial *P. X vitifolius* for these hybrids between *P. frigidus* var. *palmatus* and *P. sagittatus* (= *P. frigidus* var. *palmatus X P. sagittatus*; *P. warrenii*).

Britton's *Petasites gracilis* from the Upper Yukon District has a rounded leaf blade and shallow teeth. Cronquist's (1946) synonymized that name with the typical variety of *P. frigidus*.

Petasites alaskanus (Rydb.) is based on a specimen from St. Paul's Island. It represents *Nardosmia frigida* var. *palmata* Herder in part (Rydberg 1927). The blades are more rounded than those of *P. frigidus* var. *frigidus sens. strict.* Additionally, there are approximately seven shallow lobes with coarse dentate teeth, and the basal lobes are incurved.

Petasites nivalis Greene is distinguished from other taxa by its much divided foliage, cordate outline, and oblong and closed sinuses. Greene (1889) described this specimen from Mt. Rainier. The type description reads "20 August, 1989, Crater Lake, lamina 3-6 inches long". Such a specimen could not be located, however. The label on the designated lectotype is dated 21 August and the leaves are less than six inches in length. Nevertheless, it is believed that this specimen was of the original material examined by Greene. In 1953, Cronquist made the new combination *P. frigidus* var. *nivalis*. Toman (1972), however, retained this taxon at the specific rank of *Petasites nivalis* Greene along with two subspecific entities in addition to the typical one. *Petasites nivalis* subsp. *hyperboreus* was based on the type of *P. hyperboreus* Rydb. and *P. nivalis* subsp. *vitifolius* was based on the type of *P. vitifolius* Greene.

In 1927, Rydberg proposed the new taxon *Petasites hyperboreus*. He stated that this taxon was based on *Nardosmia corymbosa* Hook. mainly, *N. frigida* var. *corymbosa* Herder, and *P. corymbosa* (R.Br.) Rydb. Examination of the type of *P. hyperboreus* has found it to be remarkably similar to the type of *P. nivalis* Greene.

Hultén (1937) proposed a new variety of *Petasites* called *P. frigidus* var. *hyperboreoides* in his Flora of the Aleutian Islands. It has a leaf form which approaches that of *P. hyperboreus* but is less dissected. He postulates that such forms with intermediate morphologies between *P. frigidus* (L.) Fries and *P. hyperboreus* Rydb. are the result of hybridization between these two taxa. He maintains that *P. alaskanus* Rydb., *P. arcticus* Porsild, and *P. frigidus* var. *nivalis* (Greene) Cronq. in part, represent additional polymorphic variants of these hybrid intermediates (Hultén 1950). In his 1937 publication, Hultén did not designate a type specimen for *Petasites frigidus* var. *hyperboreoides* as it was not yet required by the ICBN. However, in his Flora of Alaska and Yukon (1950), Hultén provided an outline drawing of a specimen from Unimak I. and referred to it as the type specimen. Therefore, it is a lectotype. The drawing most closely resembles *P. alaskanus* Rydb.

Careful inspection of all of the type specimens, in combination with personal field observations of populations of *P. frigidus* var. *frigidus*, suggests that all of these specimens are of the same very polymorphic entity.

DESCRIPTION

Perennial, from a creeping rhizome, *basal leaves* 2-25 cm long and 2.2-27 cm wide (Bogle 1961), blade sagittate, deltoid, reniform to cordate, margin only dentate or lobed, if only dentate, up to 22 teeth present, if lobed up to 14 primary lobes, entire or dentate, and 0-25 secondary entire or irregularly toothed lobes present, shallowly lobed or deeply parted, in extreme forms lobes with at least 2 lateral triangular teeth, lobes often overlapping, sinuses oblong and closed, sinuses up to 5.2 cm deep and up to 2.1 cm wide, adaxial surface

tomentose, abaxial surface glabrous to woolly; *staminate heads* 2-20, phyllaries 3.6-10.7 mm long and 1-4.4 mm wide, phyllary margin entire to serrate, pappus length of ray florets as long as 7.5 mm, peripheral ray florets 1-13, rays 1.6-12 mm long and 0.1-3.8 mm wide, style 2.8-10.7 mm long, style branches 0.1-1.5 mm long, style texture papillose to hairy, pappus of disc florets 1.4-6.9 mm long, disc florets 16-78, corolla 2.4-6.1 mm long, corolla lobes 0.8-2.6 mm long and 0.3-4 mm wide, corolla lobes triangular, style 3-15.8 mm long, style branches 0.05-2 mm long, style texture papillose to hairy, anthers 0.5-2.9 mm long, anther apical appendage round to triangular; *pistillate heads* 5-19, phyllaries 1.67-8.83 mm long and 1.08-3.33 mm wide, phyllary margin serrate, pappus length of ray florets as long as 15 mm, ray florets 30-109, rays 0.8-4.8 mm long and 0.10 to 1.2 mm wide, style 4.6-10 mm long, style branches 0.08-0.60 mm long, style texture papillose to hairy, pappus length of disc florets as long as 0.5-8.3 mm, central disc florets 1-12, corolla 0.3-6.8 mm long, corolla lobes 0.36-4.4 mm long, 0.2-0.8 mm wide, corolla lobes rounded or triangular, style 2.6-8.3 mm long, style branches 0-1.24 mm long, style texture papillose to hairy, anthers 0.4-1.52 mm long, anther apical appendage mostly triangular; *achenes* up to 2.7 mm long; chromosome numbers 2 n = 60 and 3 n = 90.

HABITAT AND DISTRIBUTION

Petasites frigidus var. *frigidus* commonly occurs along moist alpine and subalpine slopes, along streams, in marshes, and at edges of moist *Populus tremuloides, Picea,* and *Salix* forests in addition to gravelly or sandy roadsides. Although frequently found at high altitudes, it also occurs at lower altitudes of approximately 1050 m (Bogle 1961).

The geographical range of this taxon extends from northwestern North America to Eurasia. It ranges from Spitsbergen eastward to Kolgujev and Novaya Zemlya, south to Denmark, Norway, Sweden, Iceland, and across Europe and Asia (Hultén 1950). In North America, var. *frigidus* is dominant in Alaska, Yukon, the Northwest Territories and several Arctic

islands including Banks Island, Victoria Island, Prince Patrick Island, Melville Island, St. Lawrence Island, St. Matthew Island, Nunivak Island, Kodiak Island, and St. Paul's Island. Extreme leaf forms of this taxon, which are highly lobed and dissected, are absent from the Arctic and east Keewatin District in the Northwest Territories. The distribution of var. *frigidus* continues southward to British Columbia, Alberta, and Washington. See Figure 3-2.

REPRESENTATIVE SPECIMENS

CANADA. Alberta: Banff National Park, vicinity of Sunshine Lodge south of Healy Creek, Twin Cabin Mt., *A.E. Porsild and J. Lid 19684* (CAN); Banff, vicinity of Lake Louise, in boggy places along west end of Lake Agnes, *A.E. Porsild and J. Lid 12864* (CAN).
British Columbia: Vancouver Island, Burman Mt., stream bed with *Mimulus, Epilobium, B.W. Davies and R.A. Keller 1810* (CAN); Robb Lake, slopes on north side of lake, *G.W. Argus and E. Haber 10321* (CAN); North side of lake known locally as Glacial Lake, at foot of Glacial Mtn., Cry Lake map sheet, Cassiar District, *L. Donovan and C. Sienes 951* (UBC); Birch Mtn., Teresa Island, Atlin Lake, northwest slope, *S. Buttrick 507* (UBC); Lake Takakia about 10 miles south of Moresby Logging Camp (head of Cumshewa Inlet), Moresby Island (Queen Charlotte I.), *J.A. Calder and R.L. Taylor 36268* (UBC); Mount northwest of Eve River, easternmost extension of Tsitika River Drainage, Northeast Vancouver Island, *H. Roemer 200* (UBC); Tundra at Mosquito Flats, Mile 68, Haines Highway, Haines Cut-off, *L. Hamet-Ahti 567* (WIS).
Northwest Territories: Queen Elizabeth Islands, western Melville Island, Stevens Head, *S.A. Edlund 447* (CAN); St. Patrick Island, Mould Bay, moist slope of south exposed hill, *S.D. MacDonald 168* (CAN); Great Bear Lake: scented Grass Hills Peninsula, south shore of Etacho Point, *A.E. Porsild 1432* (CAN); Camp Franklin, at origin of Great Bear River, *A.A. Lindsy 392* (CAN); Peat bog area of Mackenzie Delta near Inuvik, *s.n.* (UBC - V171428).
Yukon Terrritory: Porcupine River, 35 miles N.E. of Old Crow, *L. Hettinger 232* (ALTA); 90 miles N.W. of Dawson City, in valley 1 mile S.E. of Mt. Klotz, approx. 1/2 mile below the terminal moraine, *C. Greene 405* (ALTA); Ogilivie Mts., along Dempster Road, Mile 44-46, *R.T. Porsild 1432* (CAN); Keno Hill, south-facing rich herbmat slopes, in wet places, *R.T. Porsild 767* (CAN); Mt. Nansen, 40 miles west of Carmacks, in wet alpine tundra, *R.T. Porsild 1384* (CAN); Canol Road: Granite Mountain range west of Upper Rose River, opposite Mile 95, alpine slopes and ravine from timberline (5000') to summit (6700'), *A.E. Porsild and A.J. Breitung 10229* (CAN); Blow River, river flats behind wet delta area, *S.G. Aiken and K.I. McLachlan 87-244* (CAN); Sleepy Mountain, north-facing slope, Site 3, *S.G. Aiken and K.I. McLachlan 87-180* (CAN); Near Bear Creek Summit (Mile 1028), ca. 3000 ft., *W.B. Schofield and H.A. Crum 7894* (UBC); Lapie Lakes, in willows, *K. Beamish, D. Krause, and J. Luitjens 681353* (WIS); Mountain slopes east of the mouth of Slim's River, Kluane Lake, wet turf in alpine snow flush, *H.M. and L.G. Raup 12567* (WS).
U.S.A. Alaska: Near Wiseman, woodlands, *R. Brockman 25* (ALA); Livengood Quad: Wickersham Dome burn, on fireline (Line VI), in wet peat, on bank at edge of fireline, *A. Batten 76-134* (ALA); Mt. Micheslon Quad.: Kavik River headwaters, *S. Keller 1162* (ALA); Fairbanks Quad.: Killarney Lake, in white spruce grove near lake, *G.W. Argus 741* (ALA); Nushagak Bay Quad.: Walrus Islands, Round Island, *J. Sherburne s.n.* (ALA); Juneau, *J.P. Anderson 6423* (ALA); Chugach National Forest, Upper Paradise Lake 1 1/2 miles N.W. of upper end of lake, *E.*

Figure 3-2. Distribution of *Petasites frigidus* var. *frigidus* in North America. Bar = 500 km.

Helmstetter 80-200 (ALA); Endicott Mts. of Brooks Range: Arrigetch Creek Valley, wet basin of cirque, *D.J. Cooper 1080* (ALA); Ketchikan Quad.: Upper Wilson Arm-Smeaton Bay Area, meadow, *D.E. Bramlet 165* (ALA); Edge of Sphagnum bog, on bench below Telavirak Hills, c. 150' - 200', c. 2 miles south of Ogotoruk Creek, *J.G. Packer 2038* (ALTA); Barrow, U.S.G.S. T23N:R17W, Site 2 area, 25 yds. south of power pole line - 5.4 poles in from road, *G. McPherson and M. Galeski 72-246* (ALTA); Swampy place, Mt. McKinley Park, *Dutilly, Lepage, and O'Neill 20160* (CAN); McCarthy Quad: vicinity of the Guerin Glacier Terminus, upper White River valley, *D.F. Murray 2138* (CAN); St. Matthew Island, Bering Sea District, well drained mesic meadow on gentle southeast-facing slope, "Camp Lake" valley, *V.L. Harms 5362* (CAN); St. Lawrence Island, Bering Sea, arctic tundra, vicinity of Boxer Bay, *E.G. Franz Sauer s.n.* (WIS); Arctic Research Lab, Point Barrow, *M. Shields s.n.* (WIS); Kodiak Island, from top of ridge on west side of Three Saints Bay near mount., *B.H. Nybakken 1046* (WIS); Thompson Pass, Chugach Mts, Mile 25.2 Richardson Highway, in montane tundra, *L. Hamet-Ahti 567* (WIS); Falls Creek Mine near Kenai Lake, Kenai Peninsula, *J.A. Calder 6087* (WS); Port San Juan, Evans Island, wet alpine, *W.J. Eyerdam 7050* (WS); Eshamy, 24 miles S.E. of Whittier, Prince William Sound, common in patches along small streams on Sadde Peak, north exposure, *J.D. Solf 66* (WS).
Washington: Cascade Mts., *J.M. Grant s.n.* (WIS); Chehalis Co.: Baldy Park, *F.H. Lamb 1356* (WS); Whatcom Co.: grassy stream bank, 4200', Twin Lakes, *H. St. John 8887* (WS); James Lake, Mt. Rainier, 4370', *W.T. Shaw s.n.* (WS-62941).

Petasites frigidus var. ***palmatus*** (Ait.) Cronq., Rhodora 48: 124. 1946.

Tussilago palmata Ait. Hort. Kew 3: 188. 1789. *Nardosmia palmata* Hook, Fl. Bor. Am. 1: 308. 1833. *Nardosmia frigida* var. *palmata* (Ait.) Herder, Bull. Soc. Nat. Mosc. 38: 372. 1865. *Petasites palmatus* (Ait.) Gray, Bot. Geol. Surv. Calif. 1: 407. 1876. *Petasites palmatus* subsp. *palmatus*, Toman, Folia Geobot. Phytotax. Praha 7: 390. 1972. TYPE: "Croque, Nfld." (fide label), 1766, *Banks s.n.* (HOLOTYPE: BM-000201!).

Nardosmia hookeriana Nutt., Trans. Am. Phil. Soc. II. 7: 288. 1840. *Petasites hookerianus* (Nutt.) Rydb., N. Am. Fl. 34: 214. 1927. TYPE: not at PHIL or BM.

Nardosmia speciosa Nutt., Trans. Am. Phil. Soc. II. 7: 288. 1840. *Petasites speciosus* (Nutt.) Piper, Mazama 2: 97. 1901. *Petasites palmatus* subsp. *speciosus* Toman, Folia Geobot.

Phytotax. Praha 7: 391. 1972. TYPE: "forests of Columbia and Wahlemet" (fide label), *s.n.* (LECTOTYPE-designated here: BM-000200!).

Petasites arcticus Porsild, Sargentia 4: 74. 1943. TYPE: "Mackenzie River Delta: East Branch, lat. 68°40'N in wet clay of shady ravines. June 26, 1932. A. E. Porsild 6515". On TOPOTYPE: "Reindeer station, 68°42'N, 134°08'W. Rare in shade of *Alnus* and *Salix* on middle slope of Caribou Hills" (fide label), July 13, 1957, *W. J. Cody and D. H. Ferguson 10017* (HOLOTYPE: CAN-10866!).

TYPE MATERIAL AND NOTES ABOUT SYNONOMY

This taxon is sufficiently characterized by the presence of 5 to 11 palmately divided lobes. Nevertheless, numerous segregates based on slight differences in leaf morphology have been proposed. *Petasites frigidus* var. *palmatus* was first described as *Tussilago palmata* by Aiton in 1789, based on a specimen collected at Croque, Nfld. by Banks. See Figure 3-3. An illustration of Ehret's painting of Banks' plant is found in Hort. Kew 34: pl. II. In 1833, Hooker transferred *T. palmata* to *Nardosmia*.

Nuttall (1840) described 2 segregates of *Nardosmia palmata*. He described *Nardosmia speciosa* based on a specimen from Oregon. It reflected *N. palmata*, in part, but was "a larger plant, with the leaves more numerously lobed, and not so deeply cleft" (Nuttal 1840). *N. hookeriana* Nutt. was distinguished as having "leaves cordate, not very deeply palmately lobed, the divisions angular and toothed" (Nuttal 1840). Nuttal (1840) did not base this species upon one specimen but on *N. palmata* of Hooker (1833), Willdenow (1800), Pursh (1814) in part, and De Candolle (1836). Although specimens of *Nardosmia hookeriana* that could be verified as having been identified by Nuttall were not seen, his original description suggests that the morphological variability expressed by this segregate is within the confines of *Petasites frigidus* var. *palmatus*.

Figure 3-3. Holotype of *Tussilago palmata* Ait. (BM). Bar = 3 cm.

HOLOTYPE OF

Tussilago palmata Ait.

Hort. Kew. 3: 188. 1789.

Donna M. ChernLavsky 1994

The comment given below, with reference to the specimen [redacted] collected by Joseph Banks in 1766, is extracted from page 212 of LYSAGHT, A.M. "Joseph Banks in Newfoundland and Labrador, 1766", London (Faber & Faber) 1971.

†*Petasites palmatus (Ait.) A. Gray. Diary 33, n. 24. His 'Croupe'. Cat. 37 'a *Tussilago* Wood rather damp Croupe'. Solander MSS iv. 629. Fine C. pinnate pl. IX, of Banks's plant which is the type, is marked 'Croupe'; it was reproduced by Aiton (1789, 3: facing p. 188). Croupe is therefore the type locality. Aiton mentions Labrador as well as Newfoundland as the habitat but there is no Banksian material of *P. palmatus* from Labrador; Aiton (i.e. Solander) probably made an error in determining the Moravians' specimen of *P. frigidus*, which is not mentioned in the Solander MSS, and assumed that both specimens were *P. palmatus*.

PLANTS OF NEWFOUNDLAND AND LABRADOR

COLLECTED BY JOSEPH BANKS IN 1766

Type

Petasites palmatus (Ait.) Gray

Rather damp wood

Croupe Newfoundland

Coll. Joseph Banks

Herder combined *Nardosmia palmata* as a variety with *Petasites frigida* in 1865 although he did not acknowledge *N. speciosa* or *N. hookeriana* in his treatment. Whether he was unaware of Nuttall's publication or simply did not recognize them as legitimate names is not known.

The various palmately leaved species under *Nardosmia* were transferred to *Petasites* by several different authorities. *Nardosmia palmata*, *N. speciosa*, and *N. hookeriana* were transferred to *Petasites* by Gray (1876), Piper (1901), and Rydberg (1927), respectively.

Porsild described *Petasites arcticus* for the supposed endemic species of *Petasites* in the Mackenzie Delta region and Richardson and Mackenzie Mountains. Distinguishing features of this taxon included glabrous leaves, highly dissected lobes, and deep sinuses. Such characters are hardly constant, however, as was noted by Hooker (1833) when he stated that the leaves become "perfectly glabrous" with age.

Cronquist (1946) followed Herder's (1865) circumscription and made the new combination *Petasites frigidus* var. *palmatus* (Ait.) Cronq. He placed the above mentioned segregates, excluding *P. arcticus* in synonomy under this variety.

Toman's concept of this taxon was not as an infraspecific component to a species, but as a distinct species with its own infraspecific taxa (1972). The subspecific autonym *Petasites palmatus* subsp. *palmatus* was based upon Aiton's type. *Petasites palmatus* subsp. *speciosus* was based on the type of Nuttall. Toman (1972) placed *Petasites arcticus* Porsild in synonymy under *Petasites nivalis* subsp. *hyperboreus*.

After comparing all the type specimens and from personal observations of morphological leaf variation in natural populations, the slight diversity of leaf form is interpreted to be within the natural variation of the group.

DESCRIPTION

Perennial, from a creeping rhizome, *basal leaves* 2-40 cm long and 3.9-50 cm wide (Bogle 1961), blade orbicular, deeply cordate to reniform; margins palmately lobed with 5-11 primary lobes, lobes may be cleft almost to center (western specimens are usually larger and are divided only abut half way to the base), up to 13 secondary lobes present in larger specimens, lobes entire to dentate with up to 52 teeth, sinuses up 8.9 cm deep, up to 2.1 cm wide, adaxial surface glabrous to pillose, abaxial surface glabrous to tomentose; *staminate heads* 4-32, phyllaries 5.7-12.8 mm long and 1.5-3.7 mm wide, phyllary margin entire to serrate, pappus length of ray florets as long as 6.3 mm, peripheral ray florets 5-70, rays 0-6.3 mm long and 0-5 mm wide, style 1.5-10.3 mm long, style branches 0.08-0.6 mm long, style texture papillose, pappus length of disc florets as long as 8.3 mm, disc florets 11-60, corolla 2.6-4.8 mm long, corolla lobes 0.7-3.8 mm long and 0.3-1 mm wide, corolla lobes rounded or triangular, style 5.7-23 mm long, style branches 0-1.7 mm long, style texture papillose to hairy, anthers 0.04-4.16 mm long, anther apical appendage round to triangular; *pistillate heads* 8-42, phyllaries 1-9.5 mm long and 0.7-2.7 mm wide, phyllary margin completely entire or serrate, pappus length of ray florets as long as 11.8 mm, ray florets 51-125, rays 0-6.3 mm long and 0-0.8 mm wide, style 1.8-9.6 mm long, style branches 0.06-0.80 mm long, style texture papillose, pappus of disc florets up to 6.9 mm long, central disc florets 1-5, corolla 2-3.75 mm long, corolla lobes 0.52-2.9 mm long, 0.2-0.6 mm wide, corolla lobes rounded or triangular, style 1.9-8.3 mm long, style branches 0-0.8 mm long, style texture papillose to hairy, anthers 0.7-1.5 mm long, anther apical appendage rounded or triangular; *achenes* up to 3.5 mm long; chromosome number $2n = 60$.

HABITAT AND DISTRIBUTION

Petasites frigidus var. *palmatus* inhabits moist clay, shale or sandy soils of disturbed sites such as road cuts, embankments, stream banks, swamps and roadsides. This plant is also

commonly found in moist woods and has been found growing in relatively dry, gravel roadsides in the Yukon and Northwest Territories.

P. frigidus var. *palmatus* is widely distributed across Canada and the northern United States. In Canada, it ranges from the northwest Yukon Territory to the west Mackenzie District south to British Columbia and eastward to Labrador, Newfoundland, Nova Scotia, New Brunswick, and Prince Edward Island. In the United States, its range extends southward to Massachusettes and New York in the east, to Michigan centrally, and as far south as Monterey County in California in the west. See Figure 3-4.

REPRESENTATIVE SPECIMENS

CANADA. Alberta: Thickets along road near McMurray, *H.M. Raup and J.H. Soper 9055* (ALA); Wet place in woods with a northern exposure, bank of Fish Creek, opposite Burnside picnic grounds, about 10 mi. S. of Calgary, *W.C. McCalla 10464* (ALTA); Goodwin Lake: Northwest tip of lake, ca. 63 mi. N. of mouth of Owl River on N. side of Lac la Biche, Twp. 74, R11-12 - W4thM, *M.G. Dumais and G.G. Rankin 1403* (ALTA); Cold Lake: French Bay E. of peninsula along the Alta-Sask border Twp. 63 R1WthM, *M.G. Dumais and G.G. Rankin 1220* (ALTA); Aspen woods, Pine Lake, *H.M. Raup 3404* (CAN); Slave Lake District, Prairie Creek, low damp spots in forest, *A.H. Brinkman 4130* (US).
British Columbia: Vicinity of Beatton River, *H.M. Raup and D.S. Correll 10031* (ALA); Mile 612, Alaska Hwy., E. of Lower Post, alt. 2000', *J.A. Calder and J.M. Gillett 24474* (ALA); Ca. 1 mile N. of Indian Head Mt. Viewpoint, Km 572 of the Alaska Hwy., roadside clearcut and ditch, *L. Marvin 2233* (ALA); In leaf mold beneath alder thickets, valley of Kicking Horse River, near Mt. Stephen, Yoho National Park, *W.C. McCalla 9273* (ALTA); Upper Peak Lake, just west of Peak lake, Northwest side of lake in wet spruce forest, *J.M. Gillett and M. Boudreau 17712* (CAN); Robb Lake, slopes on North side of lake, *G.W. Argus and E. Haber 10186* (CAN); Priestly, low places in sandy aspen woods, *T.M.C. Taylor and W.H. Lewis 379* (UBC); Spanish Banks, Vancouver, *J.W. Eastham s.n.* (UBC - 6501); Salmon River, 15 mi. N. of Prince George *J.W. Eastham s.n.* (UBC - 11706).
Manitoba: Nueltin Lake, below falls of Thlewiaza River out ot Nahili Lake, wet black spruce woods, *W.K.W. Baldwin 2281* (CAN); Assiniboine Rapids, in swamps and bogs, *J. Macoun 14673* (CAN); Head River Lake, *M. and J. Bryant s.n.* (UBC - 86964); Cochrane River, willow-alder thicket, *W.K.W. Baldwin 2112* (WU).
New Brunswick: Westmorland County: Salisbury, swamp area, *E.C. Smith, W.J. Curry, R.E. Clattenburg, and A.C. MacDonald 18757* (CAN); Moncton, damp woods, *H.J. Scoggan 12155* (CAN).
Newfoundland: Mokkovik, *Dutilly, O'Neil, and Duman 3-8-39* (CAN); Labrador: Twin Falls, *I. Hustich 80* (CAN); Labrador: Nain, wet spruce woods, *H. Bishop 597* (CAN); Labrador: Goose Bay, Alexander Lake area, sandy-gravel roadside, *J.M. Gillett and W.I. Findlay 5086* (UBC).
Northwest Territories: Mackenzie River Delta: Reindeer Station, rare in shade of *Alnus* and *Salix* on middle slope of Caribou Hills, *W.J. Cody and D.H. Ferguson 10017* (TOPOTYPE) (ALA);

Figure 3-4. Distribution of *Petasites frigidus* var. *palmatus* in North America. Bar = 500 km.

Mackenzie Lowlands: Liard River Valley, Fort Liard, *W.W. Jeffrey 181* (CAN); Mackenzie Delta: Kittigazuit, *J. Robertson 102* (CAN); Yellowknife, road to airport, moist sand of broad roadside ditch, *W.J. Cody and J.B. McCansa 3264* (CAN); East side of Canoe Lake, *J. Lambert and D. Morrison 65070303* (UBC).

Nova Scotia: Shelburne County: swampy woods, east side of Clyde River, *A.R. Prince and C.E. Atwood 1278* (WIS).

Ontario: Thunder Bay District: S. side of Expressway, 1 mi. E. of Hodder Ave., McGregor Twp., moist low springy area along small stream, *C.E. Gartgon 11388* (CAN); Cochrane District: Hearst, 8 miles Northwest of Hanlan Township, clearing in spruce-poplar woods, *W.K.W. Baldwin 5634* (CAN); Kenora District: Windigo Lake, east side of lake along #599, west side of road, *A. Vogg 1496* (CAN); Ojibway Provincial Park: near Sioux Lookout, mesic sprucce-fir upland, *R. Anderson s.n.* (WIS); 18 miles S. of Red Lake on Hwy. 105, old growth *Picea* forest, *M.J. Lechowicz and W.M. Post III, s.n.* (WIS).

Prince Edward Island: Prince County: Alberton, wet woods, *M.L. Fernald and H. St. John 8238* (CAN); Brackley Point, swamps and bogs, *J. Macoun 16,661* (CAN).

Quebec: Opinaca Lake Quad.: Eastman River, 42 mi. E. of East Main, Forestry Sv. Locality No. 145, *Picea mariana*, feather-moss forest on a marine clay terrace above the river, Stand No. 149-P, *G.W. Argus 9273* (CAN); Morhiban Lake, Mecatina, *I. Hustich 1162* (CAN); Morin Heights, *F.F.M. Victorin and R. Germain 70065* (WS).

Saskatchewan: Wallwort, moist ground, *A.J. Breitung 401* (CAN).

Yukon Territory: Cut over, lodgepole pine woods, at Mile 740.5 Alaska Hwy., *S.L. Welsh and G. Moore 7573* (ALA); Watson Lake, *J.P. Anderson and R.G. Brown 9939* (CAN); Dempster Highway at Eagle Plains, exposed area around motel, *V.E. McNeilus 87-693* (US); Watson Lake, 2 mi. E. of the town centre, Alaska Hwy. Mile 632, by public campground, *L. Hamet-Ahti 1355* (WIS); Rancheria, Alaska Highway 710, *J.P. Anderson 10413* (WS).

U.S.A. California: Santa Clara County: Alma, *C.F. Baker 371* (UBC); Monterey County: Santa Lucia Mountains, *R.A. Plaskett 31* (US); Mendocino County: Round Valley, alt. 440 m, *V.K. Chestnut 222* (US); Santa Cruz County: About 1/2 mile S. of Glenwood along Bean Creek, alt. about 880 ft., moist shaded area along creek in Redwood-Douglas Fir region, *J.W. Thomas 1441* (US).

Minnesota: Cook County: toward east end, south shore of Mountain Lake, Twp. R.2E, *F.K. Butters, G.W. Burns, and M.J. Hendrickson 60* (US); St. Louis County: Highland, *E.P. Sheldou s.n.* (WS - 29025); Itasca Park, *R.W. Dawson s.n.* (WS - 257905).

New York: Canton, *O.P. Phelps 1017* (CAN).

Oregon: Coos County: in moist, shaded ravine, above Hwy. 42, S.W. of Remote, *A.N. Steward 6023* (UBC); Columbia County: railway embankment, 5 mi. E. of St. Helens, *J.W. Thompson 4003* (US); Lincoln County: Cape Perpetua, near Hwy. 101, wet roadcut, *A.N. Steward 6646* (WS).

Washington: Mt. Baker, Glacier Creek Rd., rocky roadside, *F. Vrugtman 1669* (UBC); Kittitas County: along banks of Swauk Creek near Liberty, Wenatchee Mts., *J. W. Thompson 14503* (TOPOTYPE) (UBC); Kittitas County: Liberty, Swauk Creek District, in wet clay soil, *J. Eyerdam 1502* (TOPOTYPE) (WIS); Clallam County: head of trail to Cape Flattery, roadside, pacific rainforest, *G. Hart 285* (WS); King County: along high water bank of Big Creek , *A.R. Kruckeburg 2929* (WS).

Wisconsin: Ashland County: Apostle Islands, Michigan Island, *G. Cottam and R.J. Vogl 518* (WIS); Bayfield County: Lake Superior region near Drummond, *L.S. Cherry 4237* (WIS); Oconto County: (T.29N; R.18E; Sect. 27) N.W. of S.W., Tn of Maple Valley, *E.J. Judziewicz 1803* (WIS).

Petasites frigidus (L.) Fries var. ***sagittatus*** (Banks ex Pursh) Cherniawsky, *comb. et stat. nov.*

Tussilago sagittata Banks ex Pursh, Fl. Am. Sept. 531. 1814. *Nardosmia sagittata* (Banks ex Pursh) Hook, Fl. Bor. Am. 1: 307. 1833. *Petasites sagittatus* (Banks ex Pursh) Gray, Bot. Geol. Surv. Calif. 1: 406-407. 1876. TYPE: "Hudson's Bay near Fort Albany" (fide label), 1781, *Hutchinson s.n.* (HOLOTYPE: BM-000202!).

Petasites dentata Blankinship, Mont. Agr. Coll. Stud. I: 102. 1905. TYPE: "Columbia Falls" (fide label), June 5, 1893, *R. S. Williams 344* (LECTOTYPE-designated here: MONT!; ISOLECTOTYPES: NY!, US-287952!).

TYPE MATERIAL AND NOTES ABOUT SYNONYMY

Tussilago sagittata is the manuscript name of Banks which was validly published by Pursh in 1814 and is based on the specimen collected by Hutchinson at Hudson's Bay. Pursh described the leaves as being "interrimis" (absolutely entire). This coincides with the type specimen (Fig. 3-5). However, it is in discordance with Hooker's description for his new combination *Nardosmia sagittata* (1833). Hooker described this plant as having dentate leaf margins.

Gray (1876) later transferred the genus *Nardosmia* to *Petasites*. His circumscription of this taxon included *Tussilago sagittata*, *N. sagittata sensu* Hooker, and *N. frigida* in part.

In 1905, Blankinship proposed the segregate, *Petasites dentata*, to include those forms with dentate leaf margins. This name was synonymized with *P. sagittatus* by Rydberg in 1927.

From personal observation of individual plants which possess leaves with both entire and dentate leaf margins it is believed that *Petasites sagittatus* and *P. dentatus* convarietal. A new combination and new status is proposed to include this taxon as an infraspecific variant of

Figure 3-5. Holotype of *Tussilago sagittata* Banks ex Pursh. (BM). Bar = 3 cm.

HOLOTYPE OF

Tussilago sagittata Banks ex. Pursh

Fl. Am. Sept. 531. 1814.

Donna M. Cherniawsky 1994

Type Specimen

P. frigidus. The correct name for this taxon is *P. frigidus* (L.) Fries var. *sagittatus* (Banks ex Pursh) Cherniawsky *comb. et. stat. nov.*

DESCRIPTION

Perennial, from a creeping rhizome, *basal leaves* 1.9-34 cm long and 3.5-30 cm wide (Bogle 1961), blade sagittate, spade-shaped, deltoid to cordate, apices acute to obtuse, margins entire to wavy to dentate with up to 60 teeth, not lobed, adaxial surface glabrous to tomentose, abaxial surface villous to extremely woolly; *staminate heads* 8-35; phyllaries 6.2-9.8 mm long and 1.3-3.3 mm wide, phyllary margin entire to serrate, pappus length of ray florets as long as 6.3 mm, peripheral ray florets 4-19, rays 1.1-7.7 mm long and 0.9-4.4 mm wide, style 4.3-8.7 mm long, style branches 0-0.5 mm long, style texture papillose to hairy, pappus length of disc florets as long as 6 mm, disc florets 22-56, corolla 0.4-4.6 mm long, corolla lobes 1.2-2.2 mm long and 0.3-3 mm wide, corolla lobes triangular, style 5.6-14 mm long, style branches 0.5-2.3 mm long, style texture hairy, anthers 1.4-3.8 mm long, anther apical appendage triangular; *pistillate heads* 6-34, phyllaries 3.8-8.5 mm long and 1-3.1 mm wide, phyllary margin serrate, pappus length of ray florets as long as 17.3 mm, ray florets 31-139, rays 0.6-5.4 mm long and 0.14 to 0.8 mm wide, style 3.9-9.8 mm long, style branches 0.1-0.4 mm long, style texture papillose, pappus length of disc florets as long 11.3 mm, central disc florets 1-5; corolla 1.6-3.8 mm long; corolla lobes 0.4-1.8 mm long and 0.24-0.6 mm wide, corolla lobes triangular or intermedite between rounded and triangular, style 1.2-9.2 mm long, style branches 0.3-1.3 mm long, style texture hairy, anthers 0.7-1.3 mm long, anther apical appendage round or triangular; *achenes* up to 2.8 mm long; chromosome number 2 n = 60.

HABITAT AND DISTRIBUTION

Petasites frigidus var. *sagittatus* thrives under very wet conditions. Many plants grow in shallow standing water and in bogs, fens, marshes, marshy tundra, alluvial flats and along moist

roadsides and disturbed sites such as clearcuts. *Petasites frigidus* var. *sagittatus* is additionally found growing in association with var. *palmatus* and *P. frigidus* var. *X vitifolius* in moist woods and forest edges. It has been observed growing at elevations as high as 3,000 m (Bogle 1961).

The geographical range of *Petasites frigidus* var. *sagittatus* parallels that of var. *palmatus* although it extends into Alaska and not into California. Its distribution includes Alaska, the Yukon, the Mackenzie District to Hudson's Bay, Quebec, New Brunswick, Ontario, Manitoba, Saskatchewan, Alberta, and British Columbia. It continues southward to northeast Washington, northern Idaho, Montana, Wyoming, Colorado, North Dakota, South Dakota, northern Minnesota, North Wisconsin, and northern Michigan. See Figure 3-6.

REPRESENTATIVE SPECIMENS

Canada. Alberta: Border of tamarack bog, south of Hondo, *E.H. Moss 9006* (ALTA); Shore of smalll lake in muskeg, Caribou Mt., S. slope, *E.H. Moss 9372*; Mercoal, *E.J. Woollven, s.n.* (ALTA - 18468); Walk from Nicholl's Creek to Elkwater Lake, Cypress Hills Prov. Park, *R.G.H. Cormack 84* (ALTA); Ditch 1/2 mile E. of Ft. Saskatchewan, *G.H. Turner M.D. 1644* (UBC).
British Columbia: Vicinity of Beatton River, *H.M. Raup and D.S. Correll 10029* (ALA); Fort St. John, roadside ditch, *J.M. Gillett and D.A. Mitchell 3022* (UBC); Wet meadow along 192 Rd. (road to Pink Mt. Summit) ca. 0.5 km from Jct. with Alaska Hwy. at village of Pink Mt., *G.B. Straley and K.W. Nicholls 6208* (UBC); Marsh, Stikine River basin, north end of Eddontenajon Lake, *W. Gormon 514* (UBC); 20 miles by road N.W. of Houston along road to Smithers, *J.A. Calder, D.B.O. Saville and J.M. Ferguson 15276* (US); Manson Creek Village, N. of Ft. St. James, Alt. 3300', *J.A. Calder, D.B. Saville, and J. Ferguson 13677* (WS).
Manitoba: Woods Polish Grid, WNRE Control Area, *T. Campbell C96* (ALTA); York Factory: clearings by Hudson's Bay post in Silurian formation, *H.J. Scoggan 5935* (CAN); Fort Churchill, wet, calcareous soil in open white spruce forest, *J.C. Ritchie 1650* (CAN); 1 mile S. of Minnedosa, wet margin of pothole, *W.H. Kiel Sr. 86* (WIS); Cape Merry, 1/4 mile S. of the mouth of the Churchill River, N. of Churchill, *B. Alverson 896* (WIS); Churchill District, Gillam, *W.B. Schofield 902* (WS).
Northwest Territories: Base of Caribou Hills, East Channel of Mackenzie River about 15 miles N.W. of Reindeer Station, *W.J. Cody and D.H. Ferguson 9723* (ALA); District of Mackenzie, Mile 84 of Mackenzie Hwy., *S.S. Talbot 2186* (ALTA); Mackenzie Bison Sanctuary, *D.L. Smith 87-47* (ALTA); West side of Bathurst Inlet: in willow thicket near shore of second lake, *J.P. Kelsall and E.H. McEwan 267* (CAN); Aklavick, elev. 25 ft., *V.J. Krajina s.n.* (UBC - 196443); Wood Buffalo Park, Mackenzie Basin, base of eastern slope of Caribou Mts., grassy slough, *H.M. Raup 3420* (US); Fort Smith region, in transition areas between the sedge depressions and drier, elevated ridges, *G.B. Kolenosky 200* (WIS).
Ontario: Vicinity of the mouth of the Niskibi River, wet turfy margin of small tundra pool about 1/4 mile inland, *D.R. Moir 2319* (CAN).
Quebec: Fort Chimo area, sandy area at camp, in moist depression, *B. Boivin 2267* (US).

Figure 3-6. Distribution of *Petasites sagittatus* in North America. Bar = 500 km.

Saskatchewan: Candle Lake, *J.W. Eastham s.n.* (UBC - 108420); Cypress Hills, below beaver dam on Boiler Trail, *A.C. Budd and K.F. Best 2619* (WIS).
Yukon Territory: Dezadeash Quad.: Haines Cutoff Hwy., 148 miles from Haines, in pond, *Juneau Botanical Club 130* (ALA); Mile 667 of Alaska Hwy., willow-black spruce muskeg, *S.L. Welsh and G. Moore 7480* (ALA); Vicinity of Halfway Lake: North of Mayo, elev. 2300 ft., lakeshores and swampy flats, *R.T. Porsild 494B* (CAN).
U.S.A. Alaska: Fairbanks Quad.: College, College Ave. and Farmer's Loop Rd., open boggy area, *P. Rutledge 105* (ALA); Small Lake, East side of lake shore, *S. Shelter 854* (ALA); Big Delta Quad.: Salcha River, 12 km up the river from the bridge at Mile 323.1, Richardson Hwy., *J.R. Grant 88-114* (ALA); Big Delta Quad.: Shaw Creek Flats, lake at N.E. corner, in sedge peat in wet sedge meadow at lake outlet, *A.R. Batten, G.P. Juday, and A.D. McGuire 85-9* (ALA); Gakona, *J.P. Anderson 8619* (CAN).
Colorado: Banks of Clear Creek, *H.N. Patterson 27835* (WIS).
Michigan: Schoolcraft Co.: growing in grass-sedge swale with alder and bog birch, ca. 9 1/2 miles E. of Shingleton, *D. Henson 1814* (WIS).
Montana: Bozeman, *J.W. Blankinship s.n.* (US - 668712).
North Dakota: Bottineau Co.: in wet depression, at edge of woods, near Lake Metigoshe, Turtle Mts., *V.E. Rudd 677* (US).
Washington: Pend Oreille Co.: wet meadows, near Pee Wee Falls, NW 1/4 Sec. 22, T4ON, R43EWM, 2500', *E.F. Layser 606* (WS); Okanogan Co.: wet meadow near Wauconda Summit, alt. 3500', *J.W. Thompson 8641* (WS); Spokane Co.: Latah Creek, *W.N. Suksdorf 12876* (WS); Ferry Co.: Kelete Range, Colville Nat. Forest, Thirteen Mile Area, marshy ponds at headwaters of Thirteen Mile Creek, 35N R33E Sen 1/4 Sec. 25, elev. 4150', *P.M. Anderson and C.R. Annable 4338* (WS).
Wyoming: NW corner of Sheep Mt. along Wyo. Hwy. 11, 1.9 mi. S.W. of Wyo. Hwy. 130, R77W, T15N, SE 1/4 Sec. 8, locally abundant in partial shade in a marsh with *Carex, Salix, Betula, Alnus,* and *Populus tremuloides*, elev. 7900', *B.E. Nelson and L. Nelson 1207* (CAN); Albany Co.: in a swamp, Pole Mt. region, elev. 8300', *C.L. Porter 4186* (US); Pole Creek, *A. Nelson 81* (WS).

Petasites frigidus* var. *X vitifolius (Greene) Cherniawsky, *comb et stat. nov.*

Petasites palmata (Ait.) Gray var. *frigida auct. non* (L.) Fries: Macoun, Cat. Canad. Pl. III. 553. 1886. TYPE: Kicking Horse Lake, B.C., *J. Macoun.* Not at US.

Petasites trigonophylla Greene, Leaf. Bot. Observ. Crit. 1: 180. 1906. TYPE: Minnesota, "wet meadows, very local. N.P. Junction, Carlton Co." (fide label), June 11, 1891, *J. H. Sandberg 155a* (LECTOTYPE-designated here: US-45058!).

Petasites vitifolia Greene, Leaf. Bot. Observ. Crit. 1: 180. 1906. *Petasites X vitifolius* (Greene) Bogle, Rhodora 70: 548. 1968. *Petasites nivalis* subsp. *vitifolius* (Greene) Toman, Folia Geobot. Phytotax. Praha 7: 390. 1972. TYPE: "Emerson, Man." (fide label), June 10, 1880, *John Macoun s.n.* (HOLOTYPE: US-219559!; ISOTYPE: CAN-108757!).

Petasites warrenii St. John, Research Studies of the State College Washington 1: 109. 1929. TYPE: "Wet soil along Swauk Creek near Liberty, Kittitas County" (fide label), June 11, 1927, *F.A. Warren 542* (HOLOTYPE: WS-46229!; ISOTYPE: WS-46254!; PARATYPE: WS-46291!).

TYPE MATERIAL AND NOTES ABOUT SYNONOMY

Plants designated by this binomial have previously been named as different species and infraspecific taxa of *Petasites*. Macoun (1886) was the first person to recognize this plant as a form intermediate between *P. frigidus* var. *palmatus* and *P. frigidus* var. *sagittatus*. He considered it to be a variety of *P. palmatus* and subsequently named it *P. palmata* var. *frigida*.

In the same publication in 1906, Greene named two new taxa, *Petasites vitifolia* and *P. trigonophylla*. However, the type specimens of these plants exhibit a high degree of similarity. The type specimen of *P. trigonophylla* was designated as a lectotye instead of the holotype because the specimen lacks heads which are mentioned in the original description. It appears that Greene based his concept of this taxon on more than one specimen. It is quite certain, however, that the specimen chosen as the lectotype was of the original material used by Greene.

Petasites warrenii St. John was the name published for those plants with a limited distribution in Swauk Creek, Washington. The type of this taxon closely resembles *P. vitifolius* Greene and *P. trigonophylla* Greene.

Despite the striking similarity of these plants they were not recognized as one taxon. Cronquist (1953) placed *Petasites palmata* var. *frigida* Macoun, *P. vitifolius* Greene, and *P. trigonophylla* Greene in synonomy with *P. frigidus* var. *nivalis*. They included *P. warrenii* St. John with *P. frigidus* var. *frigidus*. Bogle (1960) finally united all of these similar forms under one name.

Through artificial crosses, Bogle (1960) provided evidence that these plants are the products of hybridization between *Petasites frigidus* var. *palmatus* and var. *sagittatus*. He discovered that not only is there interbreeding between these two taxa, but backcrossing to the parental taxa occurs as well. Furthermore, all of these hybrid entities were shown to produce viable pollen (Bogle 1968).

Bogle (1968) concluded that these plants represent phases of a large polymorphic group originating in hybridization between *P. frigidus* var. *palmatus* and var. *sagittatus*. He proposed the binomial *Petasites X vitifolius* Greene (pro sp.) to include the forms of this group. Although Toman (1972) acknowledged Bogle's (1968) work he recognized this hybrid taxon as a subspecies of *Petasites nivalis*. He named this subspecies *P. nivalis* Greene subsp. *vitifolius* (Greene) Toman.

To accomodate the new status and new name of one of the parental species (*Petasites frigidus* var. *sagittatus*) of this hybrid, the new combination, *P. frigidus* var. *X vitifolius* (Greene) Cherniawsky, *comb. et stat. nov.,* is proposed. The type specimen for this hybrid is the holotype of *P. vitifolius* (Fig. 3-7).

DESCRIPTION

Perennial, from a creeping rhizome, *basal leaves* 1.9-43 cm long and 3.5-47 cm wide (Bogle 1961), blade reniform to deltoid or mostly broadly cordate, widest at base with edges convex-curved, 4-14 shallow triangular primary lobes, 0-11 secondary lobes, lobes entire to dentate with up to 44 teeth; sinuses up to 6.9 cm deep, up to 7 cm wide, adaxial surface

Figure 3-7. Holotype of *Petasites X vitifolius* (Greene) Bogle. (WS). Bar = 3 cm.

HOLOTYPE

Parthenocissus vitifolius Greene

Bull. Bot. Observ. Crit. 1: 190. 1905.

Donna M. Chernikovsky 1994

P.F. var. PALLIATUS x P. SAUTTATUS (?)

A.L. LOGLE

13 November 1941

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glabrous to tomentose, abaxial surface glabrous to woolly; *staminate heads* 3-32, phyllaries 6.1-10.3 mm long and 1.8-9.6 mm wide; phyllary margin entire to serrate, pappus length of ray florets as long as 5.2 mm, peripheral ray floret 2-27; rays 2.1-7.8 mm long, 0.8-4.4 mm wide, style 4.3-8.7 mm long, style branches 0-0.5 mm long, style texture papillose to hairy, pappus length of disc florets as long as 6.3 mm, disc florets 16-40, corolla 2.8-9.8 mm long, corolla lobes 1.2-2.3 mm long and 0.4-1 mm wide; corolla lobes triangular, style 5.7-11.8 mm long, style branches 0.4-1.4 mm long, style texture papillose to hairy, anthers 1.2-2.6 mm long, anther apical appendage triangular; *pistillate heads* 9-34, phyllaries 3.9-6.8 mm long and 1.08-2.7 mm wide, phyllary margin entire to serrate, pappus length of ray florets as long as 7 mm, ray florets 48-89, rays 0.8-2.5 mm long and 0.2 to 0.7 mm wide, style 5.1-7.5 mm long, style branches 0.1-0.30 mm long, style texture papillose, pappus length of disc florets as long as 5.7 mm, central disc florets 1-4, corolla 2.2-3 mm long, corolla lobes 0.8-2 mm long and 0.24-0.7 mm wide, corolla lobes triangular, style 4-6.9 mm long, style branches 0.3-1.2 mm long, style texture papillose to hairy, anthers 0.8-1.3 mm long, anther apical appendage rounded to triangular; *achenes* up to 1.7 mm long; chromosome number 2 n = 60.

Bogle (1961) indicates that many juvenile forms of *Petasites frigidus* var. *X vitifolius* closely resemble the forms of *P. frigidus* var. *frigidus* which exhibit the least divided foliage. As the blade enlarges in these plants, the teeth expand to form lobes.

HABITAT AND DISTRIBUTION

Petasites frigidus var. *X vitifolius* frequently grows in association with its parental species, *P. frigidus* var. *palmatus* and var. *sagittatus*. It is most commonly found in wet, marshy conditions preferred by var. *sagittatus*.

The geographical range of this hybrid is within the confines of distribution of var. *palmatus* and *P. sagittatus*, but is narrower. It extends from the southwestern Yukon south to the United States, Washington, and eastward in Canada to northern Labrador and the Gaspé

Peninsula in Québec. In central United States *P. frigidus* var. *X vitifolius* occurs in northern Michigan and northern Minnesota. See Figure 3-8.

REPRESENTATIVE SPECIMENS

Canada. Alberta: Banff, among willows of flats of Spray River, *W.C. McCalla 9192* (ALTA); Wet place in woods with a northern exposure, bank of Fish Creek, opposite Burnside picnic grounds, about 10 miles S. of Calgary, *W.C. McCalla 10463* (ALTA); Edge of stream in woods above Elkwater Lake, Cypress Hills, *W.C. McCalla 3704* (ALTA); Edge of bog 5 miles E. and 4 miles N. of Fort Saskatchewan, *G.H. Turner M.D. 4364* (ALTA); Edmonton, border of small slough, river valley, *E.H. Moss 4219* (ALTA); Balsam poplar woods near Clive and Ponoka, *E.H. Moss 2006* (ALTA); Crimson Lake, just W. of Provincial Park, N.W. of Rocky Mountain House, *M.G. Dumais and K. Anderson 2104* (ALTA); 5 miles E. of Jasper Park Boundary along the David Thompson Highway, wet ditch by edge of woods, *M.G. Dumais and K. Anderson 2225* (ALTA); Pembina River: at campsite on Nordegg/Hinton forestry roads, damp conifer woods by the river, *M.G. Dumais and K. Anderson 2321* (ALTA); Jasper National Park: vicinity of Jasper town, moist, shaded woods along Athabasca River, *A.E. Porsild and A.J. Breitung 14455* (CAN); Muskeg of Mosser Lake Ranger Sta., *H.M. Raup 3409* (CAN); Banff National Park: Bow River Valley, Buffalo prairie between Cascade and Rundle Mts., moist, shaded places in aspen forest, elev. 4500', *A.E. Porsild and A.J. Breitung 12363* (CAN); Swampy ground, just inside Alberta boundary from Kootenay Valley, B.C., *W.C. McCalla 9560* (UBC); Poplar woods, 4 miles E. of Fort Saskatchewan, *G.H. Turner M.D. 4514* (UBC); Slave Lake District, Nr. Martin Cabin, low lying spot near creek, *A.H. Brinkman 4524* (US); White Mud Creek, near Edmonton, low place in poplar woods, *E.H. Moss 4264* (WIS).
British Columbia: Fort St. John, spruce woods, *E.H. Moss 2355* (ALTA); W. side of Klappan River, 1 km N. of BCR access road, Stikine River area, 793-854 m, *W. Gorman 1019* (UBC); Low woods, S.E. of camp near Mt. Stephen, Yoho National Park, *W.C. McCalla 9336* (UBC); Maxhamish Lake, alt. 1345', *R.M. Annas, V.J. Krajina, and R.G. McMinn s.n.* (UBC - 160161).
Manitoba: Emerson, *J. Macoun s.n.* (HOLOTYPE) (US - 219559); Wasagaming, Proven Lake, Rolling Rver, woods beside river, alluvium, edge of aspen poplar, *W.K.W. Baldwin 10891* (CAN); Riding Mountain National Park: aspen-white spruce woods by Moon Lake, *H.J. Scoggan and W.K.W. Baldwin 7399* (CAN); Norway House, off north end of Laker Winnipeg: woods near Hudson's Bay Co. post, *H.J. Scoggan 4278* (CAN); Brandon, swamp near the Equipment Farm, *J. Macoun 12467* (CAN); Gilbert Plains, Tp. 25-22 W.L., wooded bog, *J.L. Parker 2319* (CAN).
Newfoundland: Labrador: Seaplane Cove, Kangalaksiorvik Fjord, *J.Schwedland s.n.* (CAN - 500269).
Northwest Territories: Wood Buffalo Park, Mackenzie Basin, base of eastern slope of Caribou Mountains, timbered muskeg, *H.M. Raup 3410* (CAN).
Ontario: Winisk, Hudson Bay Lowlands, in willow thicket, *W.K.W. Baldwin 7442* (CAN).
Quebec: Gaspe Co.: Table Top Mt., alpine meadows, alt. 900 to 1100 m, *M.L. Fernald and J.F. Collins 259* (US); Chimo, in deep grass sod, and in sand, *J.M. Gillet 5054* (US).
Saskatchewan: Tisdale, *A.J. Breitung 1794* (ALTA); 4 1/2 miles W. of McKague, moist aspen woods, *A.J. Breitung 556* (CAN).
U.S.A. Michigan: Schoolcraft Co.: growing in grass-sedge swale, E1/2 Sec 35 T46N-R16W ca. 9 1/2 miles E. of Shingleton, *D. Henson 1815* (WIS).
Minnesota: Clearwater Co.: Itasca Park, tamarack forest, road to Bear Point, *J.B. Moyle 948* (WIS).

Figure 3-8. Distribution of *Petasites X vitifolius* in North America. Bar = 500 km.

Washington: Kittitas Co.: wet soil along Swauk Creek near Liberty, *F.A. Warren 542* (HOLOTYPE) (WS); Kittitas Co.: edge of marsh on Ellensburg-Liberty highway, 15 miles S. of Liberty, *C.L. Hitchcock and V.L. Marsh 3283* (WS).

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CHAPTER FOUR

ORIGIN OF NORTH AMERICAN *PETASITES*

INTRODUCTION

Phytogeography is the study of distributional patterns of plants and the causes of those distributions. Present distribution patterns of plant taxa, in association with knowledge of past geological and glacial events, permits historical inferences to be made concerning previous distribution patterns. This is useful to the systematist because it provides an understanding of relationships and origins of taxa. When used in conjunction with additional information about relationships of taxa, acquired from various sources, hypotheses about the evolutionary development of the taxonomic group can be formulated. Such hypotheses are fundamental to the classification of taxa.

Based on the results obtained from the various analyses in this study and the present distribution of *Petasites* in North America, a hypothesis for the origin of North American taxa of *Petasites* is proposed. The phytogeography of *Petasites* is discussed in reference to past glaciation events, and an additional hypothesis is proposed for the evolution of the other taxa of *Petasites* in North America from the original colonizing progenitor.

Progenitor of North American *Petasites*

In this revisionary study of *Petasites*, the integration of information obtained from cytological, morphometric, and enzyme analyses has provided valuable insight into the mode of speciation and time since speciation events occurred in *Petasites*. The relatively high values of genetic identities between the different taxa of *Petasites* and the similarity in isozymes, and chromosome number, in accordance with the close morphological associations of the taxa is suggestive of a rapid and recent origin in North America. The lack of divergence at isozyme loci between taxa is interpreted to be the product of insufficient time for the accumulation of allelic

differences. Similarly, the absence of unique alleles in *P. frigidus* var. *X vitifolius* indicates this hybrid is also of recent origin.

On the basis of these interpretations and the current distribution patterns of taxa in North America, it is proposed that var. *frigidus* is the ancestral taxon of North American *Petasites* and the other taxa have diverged from it through a process of rapid adaptive radiation. The circumpolar distribution of var. *frigidus* in addition to the possession of two unique alleles is consistent with this hypothesis. Preceding the discussion of the origin of *Petasites* taxa in North America is the postulation of an origin for their proposed progenitor, var. *frigidus*.

A hybrid origin for *Petasites frigidus* var. *frigidus* has been suggested. The high degree of morphological variability exhibited by this group indicates that it may have originated through introgressive hybridization events of two more species. It is possible that the putative parental species of var. *frigidus* may not be contemporary. However, European and Asiatic specimens of *Petasites* have not been examined. Therefore, the possibility of the parental forms currently existing in these regions cannot be precluded. The origin of North American *Petasites* is further discussed in relation to the phytogeography of the genus.

Phytogeography of *Petasites*

The present distribution of *Petasites* in North America (Figs. 3-2, 3-4, 3-6 and 3-8) is explained as resulting from glaciation that occurred during the late Wisconsinan, approximately 23,000 to 10,000 years ago (Matthews 1979). The southern and northwestern limits of its range approximate the boundaries of the most recent continental glaciers. This is indicative of a previous distribution pattern that had been eradicated by the last glaciation.

Organisms survive glaciation in unglaciated regions at glacial boundaries, and unglaciated regions surrounded by ice (Matthews 1979). Such refugia have played a significant role in the survival of organisms during glaciation, and also as dispersal centers after glaciation.

An important refugium is Beringia. This includes the unglaciated parts of Alaska, the Yukon, east Siberia, and the land bridge between east Siberia and North America that was created by the exposed sea floors of the Bering Sea and Chukchi Sea (Matthews 1979). This connection was not broken until just before 13,000 years before present (Matthews 1979). Beringia not only served as a refugium for the survival and subsequent migration of organisms but acted as a vehicle for floral and faunal exchange between Asia and North America. Beringia is of paramount significance for North American taxa of *Petasites*.

Petasites probably originated in Asia and var. *frigidus*, or its precursor, used Beringia as a refugium and a dispersal route from eastern Siberia to North America during the Wisconsinan glaciation (approx. 10,000-75,000 y.b.p; Seyfert and Sirkin 1979). Support for this hypothesis is indicated by: 1) the center of maximum diversity for *Petasites* is Asia; 2) the circumpolar distribution of var. *frigidus*, it is the only taxon of *Petasites* found in Europe, Asia, and North America, and; 3) the presence of var. *frigidus* in unglaciated regions in eastern Siberia, Alaska, parts of the Yukon, and parts of Arctic Canada. Moreover, the geographical distribution of *Tussilago* includes Asia (Nordenstam 1977). If the hypothesis that *Petasites* is a derivative of *Tussilago* is accepted, an Asia origin for *Petasites* is agreeable.

Although a region of high species diversity is not necessarily the center of origin of a taxon (Johnson and Raven 1970), this has proven to be so for other plant groups (Bayer 1990). In accordance with the following information, the interpretation that Asia is the center of origin of *Petasites,* is preferred.

Of all North American taxa of *Petasites* the environment of Beringia during the Wisconsinan would have been most capable of sustaining var. *frigidus*. Beringia has been characterized as a tundra-steppe environment that was topographically and vegetatively varied (Ager 1982; Matthews 1982). Although the vegetation was composed primarily of dry tundra species, more limited habitats were available for mesic tundra species such as var. *frigidus*

(Ager 1982). Beringia could have, therefore, served as a suitable refugium and dispersal center for var. *frigidus*.

Dispersal of *Petasites* across Beringia probably did not occur as only one event, nor did it proceed in only one direction. The Bering Land bridge served as a dispersal route to the east and to the west (Brown and Gibson 1983). However, because the land bridge was in existence throughout the entire Wisconsinan (Matthews 1982) it is difficult to predict a time period when *Petasites* first used Beringia as a dispersal route.

Hultén (1937) suggested that the presence of *Petasites* in North America preceded the Yarmouth, or great interglacial (approx. 400,000-750,000 y.b.p.; Seyfert and Sirkin 1979). These plants supposedly underwent several episodes of depletion during glacial periods and expansion during interglacial periods. Hultén (1937) postulated that var. *frigidus* survived the Illinoian, or maximum glaciation (approx. 260,000-400,000 y.b.p.; Seyfert and Sirkin 1979), in refugia in east Beringia, whereas var. *sagittatus* persisted in the upper Yukon valley, south of the ice in the Rocky Mountains, at the Great Lakes, the Gulf of the St. Lawrence, and the continental shelf of eastern North America. Hultén (1937) proposed that *Petasites* expanded its range during the Sangamon or last interglacial (approx. 75,000-260,000 y.b.p.; Seyfert and Sirkin 1979), but was subsequently reduced during the last Wisconsinan glaciation. After the glaciers receded, individuals surviving in refugia would have been able to recolonize previous ranges. The more widespread distribution of var. *frigidus* currently present in Europe and Asia, as compared with North America, was explained by Hultén (1937) to be the result of more favorable refugia.

Hultén's hypothesis provides a reasonable interpretation for the most recent historic events of *Petasites*. However, a later period of occupation for *Petasites* in North America is indicated by the data about differentiation. The limited morphological and isozymic divergence among North American taxa of *Petasites* is indicative of a relatively recent and rapid evolution. Conversely, taxa exhibiting high divergence in these parameters are the result of long periods of

separation and gradual speciation. In order for North American *Petasites* to have a long evolutionary history one would expect the latter to occur. However, this is not the case.

Immigration of *Petasites frigidus* var. *frigidus* to North America could have occurred during the Wisconsinan when the Bering land bridge was in existence (approx. 10,000-75,000 y.b.p.; Seyfert and Sirkin 1979). A time closer to the upper limit of this range seems most plausible because the time of origin for other taxa also considered to have evolved recently has been estimated to be between 10,000 and 20,000 y.b.p. (Lowrey and Crawford 1985; Witter and Carr 1988). With the retreat of the glaciers, open, disturbed habitats were available for colonization by *Petasites*.

In order to expand its range, it is hypothesized that *Petasites frigidus* var. *frigidus*, characteristic of subalpine to alpine habitats, underwent a rapid process of adaptive radiation. Consequently, the evolution of ecotypes adapted to a wide array of habitats ensued. *Petasites frigidus* var. *palmatus* endured drier, more closed environments than var. *frigidus*; whereas var. *sagittatus* thrived under extremely wet conditions. The capacity of long distance seed disperal and the propensity for vegetative reproduction undoubtedly aided in the successful colonization of these habitats. With subsequent divergence, the evolution of these ecotypes proceeded toward the development of infraspecific taxa. However, divergence in habitat preference was not restricted, nor was it accompanied with reproductive isolation. Where these varieties grew sympatrically, hybridization occurred. *Petasites frigidus* var. *X vitifolius* subsequently originated as the stabilized product of hybridization between var. *palmatus* and var. *sagittatus*. Since the region of highest diversity and sympatry of all North American taxa of Petasites is in northwestern North America, this may be the region from which the first adaptive radiation events occurred.

The present distribution of *Petasites* indicates that this species survived the late Wisconsinan glaciation in refugia at the margins of ice sheets. The existence of the following

refugia of the late Wisconsinan that is proposed to have accomodated *Petasites* has been corroborated by several authors.

Petasites frigidus var. *frigidus* probably survived in eastern Siberia (Hultén 1937), Alaska (Hultén 1937; Prest 1984)), parts of north and central Yukon (Hultén 1937; Rutter 1984), parts of Kodiak Island (Karlstrom and Ball 1969), parts of Banks Island, Prince Albert Peninsula of Victoria Island, Prince Patrick Island, Melville Island (Vincent 1984), and south of the Cordilleran Ice Sheet (Rutter 1984). Refer to Figure 3-2.

Although the distribution of *Petasites frigidus* var. *sagittatus* (Fig. 3-6) suggests that it may have survived the last glaciation in east Beringia, it is possible that it is a post-glacial migrant to Alaska. The Wisconsinan environment of Beringia, believed to be predominately tundra-steppe (Matthews 1982; Cooper 1989), may not have been suitable to support this taxon characteristic of very wet habitats. Less controversial refugia include the Yukon, south of the Cordilleran Ice Sheet, the Gaspé Peninsula of Québec (Prest 1984), northern Labrador (Prest 1984), the eastern continental shelf (Prest 1984), coastal and highland regions of New Brunswick (Grant and King 1984), western Newfoundland (Grant 1977), southwest Nova Scotia (Grant 1977), and regions south of the Laurentide Ice Sheet.

Petasites frigidus var. *palmatus* exhibits a similar distribution pattern (Fig. 3-4) to var. *sagittatus* except for its absence from Alaska and the Northwest Territories. It is thus postulated that it shared similar refugia with var. *sagittatus*, although it is most likely occupied drier habitats.

Hultén (1968) and Bogle (1868) extend the distribution of var. *palmatus* to eastern Siberia. They consider var. *palmatus* to be synonymous with a palmately leaved taxon *P. tatewakianus* described by Kitamura (1940) from Sakhalin Island, USSR. These two taxa exhibit a similarity in achene length and leaf form, although lobes of *P. tatewakianus* are only dissected about one third to the center. Although specimens of this species have not been seen, a photograph of the type specimen has been observed (Kitamura 1942). It is similar in appearance to the leaves in Figs. 2-8a and 2-9 although the teeth on the lobes of *P.*

tatewakianus are more highly dissected. Possibly these leaf forms are of a similar origin. A number of hypotheses to explain the status of *P. tatewakianus* is proposed.

Petasites tatewakianus may, in fact, represent a form of *P. frigidus* var. *palmatus*. The comparable achene length and leaf form is suggestive of a close relationship between the two taxa. However, the absence of var. *palmatus* from Alaska militates against the proposal that this specimen is var. *palmatus*. Since it is reasonable to assume that taxa which originated in Eurasia and came to North American via the Bering land bridge still occupy Alaska, its absence suggests that it did not originate there, but did so in North America. There is the possibility of a previous occupation, then extripation, of var. *palmatus* in Alaska, although this seems unlikely.

It may be that *Petasites tatewakianus* is the product of hybridization between var. *frigidus* and var. *palmatus*. Possibly, the similarity to var. *palmatus* results from the introgression of genes from var. *palmatus* into var. *frigidus* where their ranges overlapped in regions such as the Yukon Territory. This is apparently a current phenomenon as the plants in Fig. 2-8 and 2-9 were collected in Alaska. Before the deterioration of the Bering Land bridge migration of these forms to Siberia would have been possible. There are no reports of chromosome numbers in *P. tatewakianus* to contribute to the understanding of relationships between it and North American *Petasites*. It is also possible that *P. tatewakianus* arose from hybridization between var. *frigidus* and one or more Asiatic species, and is therefore more closely related to var. *frigidus*. Until Asian representatives are examined one can only speculate.

The final hypothesis is that *Petasites tatewakianus* and var. *palmatus* have evolved from a common ancestor, that being var. *frigidus*. *Petasites tatewakianus* could have evolved as an ecotype of var. *frigidus* as has been postulated for var. *palmatus*. Since the habitat of *P. tatewakianus* is not known, however, it is not clear if such a suggestion is feasible.

At this time the status of *Petasites tatewakianus* is not known, although the similar morphology is suggestive of a genetic influence of var. *palmatus* on *P. tatewakianus*. Based on

the distribution of var. *palmatus* in North America, it is considered most reasonable to assume that these plants do not represent the same entity. It does seems probable, however, that the leaf form of this Asiatic species has been influenced by var. *palmatus*, possibly through hybridization with var. *frigidus*.

Petasites frigidus var. *X vitifolius* (Fig. 3-8) presently occupies a narrower range than its parents, but is most similar to var. *palmatus*. *Petasites frigidus* var. *X vitifolius* does not extend as far north or south as var. *palmatus* and it is absent from Newfoundland, southern Labrador, Nova Scotia, New Brunswick, and Maine.

CONCLUSIONS

In summary, it is postulated that North American *Petasites* originated in Europe or Asia with subsequent migrations to North America via the Bering Land Bridge during the late Wisconsinan glaciation, approximately 10,000 to 23,000 years ago. This proposal is consistent with the present distribution of taxa of *Petasites* in North America. Additionally, the genetic similarity among all taxa of *Petasites*, interpreted from electrophoretic data, is compatible with the hypothesis of a rapid and recent origin in North America. On the basis of its circumpolar distribution and the maintenance of the highest amount of genetic diversity of all North American taxa, it is proposed that var. *frigidus* is the ancestral taxon of *Petasites* in North America. It is further proposed that after the retreat of the first Wisconsinan glaciers, the other North American varieties of *Petasites* evolved from var. *frigidus* through rapid adaptive radiation events. The present geographic range of *Petasites* in North America suggests a previous, more continuous distribution pattern that had been depleted by the most recent glaciation. During the past 10,000 years, *Petasites* has been able to recolonize previously occupied regions through the exploitation of unstable habitats left by the last of the Wisconsinan glaciers. The infraspecific taxa of *Petasites* are still in the process of diverence but have not yet reached a level which isolates them as distinct species.

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CHAPTER FIVE

CONCLUSIONS

The close association of morphological characters within the various groups of *Petasites*, in conjunction with the similarity in chromosome number, and isozymes indicates that North American *Petasites* is best treated as one morphologically variable species.

Morphometric analyses achieved the separation of four ill-defined subgroups or taxa. Reproductive characters exhibited highly overlapping values over all taxa, therefore their discriminating value is considerably diminished. However, the extreme values for some characters have proven to be diagnostic for particular taxa, such as the length of style branches of disc florets in staminate inflorescences. A style branch length between 1.4 mm and 1.7 mm is diagnostic of var. *palmatus*. Similarly, a style branch over 1.7 mm is representative of *P. frigidus* var. *sagittatus* (in ed.) (Table 2-8).

The following sets of characters for reproductive inflorescences are the most taxonomically discriminating for *Petasites*. It must be emphasized that the differences between most of these characters across the various taxa are very slight, especially pistillate characters. Discriminating characters among staminate inflorescences include number of heads, style texture of disc florets, number of ray florets, and length of style branches of disc florets. The set of discriminating characters for pistillate inflorescences include number of heads, length of style branches of disc florets, phyllary margin, disc corolla lobe length, and style texture of disc florets.

Leaf characters are best able to differentiate between taxa of *Petasites*, particularly *P. frigidus* var. *sagittatus*. The absence of lobes distingushes *P. frigidus* var. *sagittatus* from the other taxa. Similarly, orbicular shaped leaves separate var. *palmatus* from the other taxa.

However, the morphological limits of each taxon is somewhat blurred as a result of overlapping character values.

The use of leaf morphology in plant identification of *Petasites* is in accordance with previous classification systems. At the onset of this study, it was hoped to obtain characters less prone to plasticity from environmental influence. Unfortunately, most reproductive characters are not discontinuous thereby reducing their discriminating potential. Thus, leaf characters in conjunction with the few reliable reproductive characters available provide the best tools with which to identify taxa. It is hoped that the revised circumscription of taxa, which is believed to reflect evolutionary relationships, will alleviate some of the ambiguity in identification of the taxa. The most discriminating leaf characters have been shown to include the number of primary lobes, sinus depth, and number of teeth.

Although, the best differentiation between the various taxa of *Petasites* has been obtained from leaf morphology, this has not been shown to be correlated with isozymic divergence. The time since morphological divergence has not been considered sufficient for the accumulation of differences at isozyme loci.

The influence of environmental factors on phenotypic variation must be considered. The impact of the environment on *Petasites* is not clear at this time, although it has been observed that the degree of dissection and number of lobes and teeth has been reduced in plants taken from the field and grown in the greenhouse. Light and temperature affect the activity of the various meristems in leaves to produce modifications in leaf dissection (Cutter 1971). These factors may influence leaf morphology in *Petasites*. Furthermore, environmental factors may act differently on minor differences in genotypes to produce variability in leaf form (Cutter 1971). Until further research is conducted, such a possibility in *Petasites* can only be speculated. At this time it is known only that morphological divergence is not correlated with isozymic divergence.

Even though results from the enzyme analysis did not prove to be useful in the delimitation of taxa of *Petasites*, this study provides the first contribution to the understanding of the population genetic structure in this clonal species. Populations of *Petasites* may exhibit levels of heterozygosity and genetic diversity more comparable to selfers than to outcrossers. Additionally, *Petasites* partitions most of its genetic diversity as selfers do; that is, among populations as opposed to within populations. This similarity to selfers is the result of the fixation of different alleles in different populations. In *Petasites* this probably arises from mating with close relatives in addition to the establishment of populations from only a few founder individuals. Genetic diversity among populations becomes further differentiated due to restricted gene flow.

The relatively high degree of genetic diversity which characterizes *Petasites* may be attributable to its ability to reproduce asexually as well as sexually. Asexual, perennial species are able to accumulate greater amounts of genetic variation than outcrossers (Cheliak and Dancik 1982). Furthermore, the ability to alternatively reproduce sexually provides a continual source of genetic variability.

Some populations of many clonal species living in heterogeneous environments become subdivided, mostly due to mating between closely related individuals (Schaal 1975; Silander 1984). Therefore, the high genetic diversity representative of clonal populations has been explained to be the result of diversifying selection. Under this process, specific genotypes associated with optimal adaptations to the the various subenvironments are favored by natural selection (Dobzhansky et al. 1977). Although some studies have determined a correlation between genetic variability and environmental diversification in some species (Burdon 1980), such correlations were not observed in other studies (Ellstrand and Roose 1987; Silander 1979).

The high genetic variablity exhibited by many clonal populations is interpreted to be the result of a combination of factors, without the exclusion of environmental heterogeneity. Selection may be operating differently on different loci in different subpopulations, thereby

contributing to the high genetic variability. Forces which can affect the genetic structure of populations include inbreeding, migration, genetic drift, competition, chance, and historical events (Schaal 1975; Silander 1979; and Burdon 1980).

This systematic treatment of *Petasites* in North America complies with the suspicions of Hooker (1833). North American *Petasites* is recognized as one highly polymorphic species, *P. frigidus*, with three infraspecific taxa. Included as varieties are *P. frigidus* var. *palmatus* and *P. frigidus* var. *sagittatus*, in addition to the typical variety, originally described as *Tussilago frigida* by Linnaeus (1753). *Petasites frigidus* var. *X vitifolius* (in ed.) is recognized as the product of hybridization between *P. frigidus* var. *palmatus* and *P. frigidus* var. *sagittatus*.

The proposed taxonomic treatment differs from the others with the transfer of *Petasites sagittatus* from the specific to the varietal rank. The close morphological association of reproductive inflorescences, in addition to the absence of reproductive barriers and isozymic similarity indicates that *P. frigidus* var. *sagittatus* is only weakly differentiated from the other taxa.

Furthermore, the previously recognized variety, *Petasites frigidus* var. *nivalis* (Greene) Cronq., has been united under var. *frigidus* along with forms intermediate in morphology between these two varieties. The close morphological association of these three groups provides a certain degree of integrity which sets them apart from the other taxa, and supports their amalgamation. Moreover, plants with leaves of both the var. *frigidus* (*sens. strict.*) and var. *nivalis* types indicate they comprise one highly variable entity.

None of the taxa of *Petasites* are considered to be sufficiently differentiated morphologically, reproductively, or isozymically, from the others to warrant the designation of the rank of species. Thus, this group is best treated as a highly polymorphic species, consisting of three varieties and one recognized hybrid.

The circumscription of *Petasites* reflects the species concept utilized in this study: "*Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means*" (Cronquist 1978). On the basis of both vegetative and

reproductive morphology the smallest group would have to include the species *Petasites frigidus*. The variation exhibited within this group is clearly assignable to *Petasites* and is discontinuous with variation from other groups, therefore, the criterion for consistency is met. Since all members of this group interbreed, the criterion for persistency is also met. Furthermore, this group is distinguishable from others by ordinary means.

The North American species of *Petasites* is believed to be derived from a European or Asian lineage. The current distribution patterns of the infraspecific taxa in North America lend support to the proposal that *Petasites* used Beringia as a refugium and dispersal route between the east and west during the late Wisconsinan. The similarity in genetic identity data obtained from the enzyme analysis is consistent with the hypothesis of a rapid and recent origin of *Petasites* in North America. Furthermore, the presence of two unique alleles, the highest number of alleles per locus, and the highest proportion of polymorphic loci in *P. frigidus* var. *frigidus*, in addition to its status as the only circumpolar taxon of *Petasites* in North America, indicate that this variety is the ancestral taxon of all North American entites of *Petasites*. Based on the synthesis of this information, it is postulated that var. *frigidus*, or its precursor, migrated from Eurasia to North America via the Bering Land Bridge approximately 10,000 to 23,000 years ago. It is probable that, in order to expand its range, var. *frigidus* underwent rapid adaptive radiation events, thereby initiating the evolution of the other North American varieties of *Petasites*.

FUTURE RESEARCH

The high diversity in leaf morphology confers the greatest contribution to the taxonomic confusion surrounding *Petasites*. At present little is known about the influence of the environment on leaf plasticity in *Petasites*.

Clearly, a detailed study of morphological variation in relation to different environmental conditions is required to understand the processes which may be operating to produce the

variable leaf morphology in *Petasites*. Transplant studies have proven to be very useful for obtaining information about the relationships between morphological variation and environments (Stebbins 1950). The clonal nature of *Petasites* is advantageous for such studies. Clones of a particular individual can be transplanted to different environments to determine if particular morphological features are in response to specific environmental conditions.

The plasticity in leaf morphology of many species may be the result of adaptations to particular environments, providing an ecological advantage if it promotes the exploitation of changing habitats. However, experimental evidence for several taxa has indicated that many morphological features are easily modifed (Cutter 1971). A particular form may not have arisen from the adaptation to a specific environmental condition, but the environmental condition may have produced the variant form. The relationship between environment and plant morphology may then be causal rather than adaptive. Such considerations in *Petasites* are worthy of investigation.

Whether or not the genetic diversity in *Petasites* is associated with environmental heterogeneity also remains unanswered at this time. Further research is needed to interpret the adaptive significance of the high genetic variablity in *Petasites*.

It is also recommended that more specimens from the entire geographic range of *Petasites* be examined electrophoretically and cytologically. Additional information would better clarify the relationships among the different taxa of North America.

For a complete understanding of the origins of *Petasites frigidus* var. *frigidus* and other North American taxa, an examination of European and Asiatic specimens is imperative. Possibly, hybridization experiments can elucidate a hybrid origin for the putative progenitor of North American *Petasites*.

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APPENDIX ONE: DATA MATRIX FOR MORPHOMETRIC ANALYSES OF LEAF CHARACTERS

MISSING DATA IS REPRESENTED BY 99, 99.0, OR 99.00.

CHARACTER	OTU																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
SHAPE	2	5	2	1	1	1	2	1	2	5	5	1	5	5	1	2	2	1	1	2
MAXW	6.10	8.00	4.80	14.20	5.90	25.00	6.40	5.00	8.50	7.20	6.20	5.40	7.20	8.00	10.10	7.10	4.90	19.30	4.00	4.80
MAXL	5.00	5.70	3.80	11.60	4.60	20.70	5.80	4.60	7.60	6.50	5.20	4.00	6.80	6.50	12.00	6.20	4.40	17.00	3.50	4.00
APWD	6.0	6.2	4.7	12.2	5.4	23.5	7.0	5.0	8.4	7.4	5.4	5.8	7.4	8.8	15.4	7.2	4.4	20.2	4.0	4.3
APANGL	60	50	47	61	58	44	6	40	45	36	40	55	44	60	30	40	51	61	48	44
BAPANGL	60	40	68	60	35	50	2	30	70	30	50	30	53	52	48	80	80	45	40	50
NO1LB	7	6	8	4	12	10	7	7	6	11	3	7	7	7	12	8	9	10	5	5
NO2LB	3	10	1	0	10	6	2	0	5	10	2	3	2	8	4	0	7	15	5	4
LBAPSHP	1.0	2.0	2.0	2.0	2.0	2.0	1.5	1.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0
NOTETH	7	9	3	32	6	7	7	9	5	15	12	9	11	16	6	15	9	20	4	9
TETHSHP	1.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	1.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0
SINDEP	1.00	1.00	0.50	1.20	1.10	4.00	1.50	0.80	1.00	1.20	0.50	0.40	0.90	1.80	1.90	0.80	1.10	2.00	0.50	0.50
SINWD	0.70	0.80	0.80	1.30	0.00	1.50	0.70	0.80	1.50	0.80	0.50	0.40	0.70	0.80	1.70	0.60	0.60	1.20	1.00	0.70
SINSHP	1.00	1.00	2.00	1.00	2.00	1.00	1.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00
PERI	24.0	32.0	16.0	59.0	24.0	95.0	53.0	25.0	32.0	47.0	24.0	23.0	29.0	56.0	56.0	24.0	19.0	51.0	17.0	17.0
PUBAD	3	0	3	0	4	0	0	0	0	5	2	0	0	3	0	0	3	99	2	0
PUBAB	99	1	4	4	3	1	4	99	1	5	2	99	2	2	2	99	99	4	4	2
LAT	60.35	68.03	70.22	64.52	60.23	61.00	60.58	63.47	69.22	51.00	62.37	60.20	57.20	60.00	61.37	66.43	60.30	61.32	99.00	75.12
LONG	139.00	145.00	150.45	147.50	166.10	116.00	138.35	145.47	152.08	170.00	143.46	152.35	159.22	137.22	141.05	138.17	152.00	159.27	99.00	117.12

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
SHAPE	1	2	1	1	1	1	1	1	1	1	2	2	2	2	2	5	1	2	1	1
MAXW	12.40	6.10	8.00	8.00	4.90	4.30	3.10	5.50	6.80	5.30	4.40	3.70	9.00	6.00	2.70	2.70	3.20	6.10	6.50	2.90
MAXL	11.10	5.00	7.00	7.50	3.00	3.60	3.10	4.30	6.00	4.50	4.20	3.10	9.60	4.50	3.20	2.50	2.70	6.10	6.00	2.80
APWD	13.3	5.6	7.7	9.6	2.9	4.2	3.0	5.1	7.4	5.7	4.6	3.2	9.7	5.8	3.0	2.7	3.4	5.5	7.3	3.2
APANGL	60	70	50	38	70	61	30	50	58	60	60	50	50	51	34	60	44	45	42	50
BAPANGL	0	60	20	16	30	30	50	41	30	40	70	60	75	54	40	70	25	70	36	30
NO1LB	8	14	6	7	11	12	6	9	13	11	9	6	3	3	6	0	9	3	9	6
NO2LB	13	3	11	6	10	14	3	12	2	12	2	0	0	0	0	0	0	0	0	2
LBAPSHP	2.0	2.0	2.0	3.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	1.0	99.0	1.0	2.0	2.0	1.0
NOTETH	11	9	4	8	2	2	11	6	9	22	2	3	9	8	0	11	2	9	5	0
TETHSHP	2.0	2.0	2.0	2.0	1.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	1.0	2.0	0.0	1.0	1.0	2.0	2.0	0.0
SINDEP	1.40	1.20	1.20	1.30	0.80	0.90	0.50	0.80	1.30	0.90	0.50	0.80	1.00	0.50	0.50	0.00	0.40	0.50	1.00	0.40
SINWD	1.00	1.20	1.10	0.70	0.70	0.50	0.40	0.50	0.80	0.30	0.50	0.80	1.20	1.00	0.50	0.00	0.70	1.30	1.10	0.70
SINSHP	1.00	2.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00
PERI	56.0	27.0	41.0	34.0	19.0	21.0	12.0	25.0	36.0	22.0	16.0	14.0	36.0	23.0	12.0	12.0	16.0	24.0	29.0	14.0
PUBAD	0	1	2	3	4	4	4	4	0	0	2	0	0	0	1	0	0	0	0	99
PUBAB	2	5	3	1	4	4	4	4	2	3	3	2	2	3	4	4	5	99	3	3
LAT	64.04	61.30	64.19	61.20	63.31	63.37	65.22	64.17	63.25	63.34	65.49	69.55	68.38	69.16	68.55	69.17	70.20	61.07	63.26	58.34
LONG	139.25	133.04	146.42	129.50	149.58	149.35	145.25	146.66	149.30	142.20	137.46	145.37	143.45	145.04	143.30	145.01	161.50	164.00	150.12	161.46

CHARACTER	OTU																			
	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
SHAPE	2	2	2	1	5	2	2	5	1	2	2	2	1	1	2	2	2	1	2	2
MAXW	4.90	9.80	7.40	5.00	5.00	3.50	2.20	10.60	6.40	10.80	3.00	4.30	3.70	5.80	2.60	2.70	3.90	5.70	9.70	5.40
MAXL	4.90	7.90	6.00	4.20	3.80	2.80	2.10	6.80	6.70	8.50	2.70	3.50	4.20	5.10	2.50	2.60	2.70	4.50	7.00	5.30
APWID	4.8	1.0	7.0	5.0	4.6	2.1	1.7	8.2	6.2	9.1	2.5	3.7	4.3	4.8	2.7	2.7	3.2	5.4	9.7	6.6
APANGL	40	60	60	50	60	50	32	52	40	55	50	50	40	31	40	40	51	44	60	48
BAPANGL	60	60	70	0	30	90	80	52	50	65	38	50	40	30	86	80	40	60	50	60
NO1LB	8	11	6	0	0	6	0	7	8	9	10	7	9	11	7	2	9	10	0	10
NO2LB	2	2	0	0	0	0	0	2	3	7	2	0	0	0	0	0	4	4	0	0
LBAPSHP	1.0	2.0	2.0	1.0	0.0	2.0	0.0	1.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	1.0	1.0	2.0	0.0	1.0
NOTETH	2	5	9	11	11	2	7	4	0	2	0	0	2	2	12	9	2	4	22	0
TETHSHP	3.0	3.0	2.0	1.0	1.0	2.0	1.0	3.0	0.0	2.0	0.0	0.0	2.0	2.0	2.0	2.0	1.0	2.0	1.0	0.0
SINDEP	0.60	1.60	0.70	0.00	0.00	0.60	0.00	1.30	0.60	1.40	0.50	0.70	0.70	0.80	0.30	0.40	0.50	0.70	0.00	0.80
SINWID	1.10	1.00	0.60	0.60	0.00	0.90	0.00	1.40	2.00	1.30	0.50	0.80	0.70	0.70	0.50	0.50	0.50	0.50	0.00	1.00
SINSHP	1.00	1.00	1.00	0.00	0.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	1.00	0.00	2.00
PERI	18.0	40.0	20.0	16.0	20.0	12.0	10.0	36.0	24.0	41.0	10.0	16.0	16.0	22.0	8.0	10.0	33.0	20.0	32.0	22.0
PUBAD	0	0	99	0	4	3	0	0	0	0	0	0	99	2	1	2	99	2	0	0
PUBAB	2	4	4	99	99	4	3	0	3	2	4	99	2	2	3	1	2	4	99	1
LAT	99.00	68.22	61.45	55.19	99.00	71.00	75.57	60.00	49.30	99.00	99.00	65.48	69.25	64.19	63.24	63.37	64.17	64.13	99.00	68.96
LONG	99.00	133.44	166.00	160.24	99.00	157.00	115.00	127.00	68.30	99.00	99.00	168.00	145.10	146.42	148.56	149.35	146.08	145.50	99.00	148.48

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
SHAPE	2	1	2	2	2	1	2	2	5	1	2	2	1	1	1	5	2	1	1	1
MAXW	9.10	4.70	8.20	4.30	6.20	5.00	11.10	4.40	5.70	6.80	4.40	4.80	5.10	6.20	5.60	16.80	4.30	9.10	7.80	8.90
MAXL	6.80	3.50	6.70	5.00	6.90	4.60	8.50	3.90	4.20	7.00	3.30	4.60	4.00	5.00	5.40	11.50	3.80	7.70	7.50	5.20
APWID	7.5	3.8	8.5	4.5	5.7	5.8	9.5	4.7	5.3	9.0	3.7	5.6	4.6	5.2	6.3	12.0	3.6	9.2	8.0	6.9
APANGL	60	40	50	32	52	50	60	55	60	30	40	60	60	60	60	47	55	60	60	41
BAPANGL	70	35	50	60	71	58	60	68	40	46	90	40	20	50	40	58	60	55	40	30
NO1LB	5	6	11	9	4	7	6	8	8	12	6	10	8	11	11	7	9	8	9	11
NO2LB	0	3	4	1	0	0	0	2	7	6	0	1	2	2	7	11	11	11	22	7
LBAPSHP	2.0	2.0	2.0	1.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	1.5	1.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0
NOTETH	6	3	13	7	10	7	8	5	9	4	4	1	9	17	0	11	8	8	7	12
TETHSHP	2.0	3.0	3.0	1.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	0.0	2.0	2.0	2.0	2.0	2.0
SINDEP	1.00	0.70	1.20	0.60	0.60	0.70	1.00	0.60	1.00	0.90	0.70	1.00	0.50	0.80	1.00	5.20	0.80	2.00	1.30	0.60
SINWID	1.30	0.70	1.00	1.00	0.70	0.70	1.00	0.70	0.80	0.50	1.20	1.00	0.50	0.80	1.00	0.70	0.30	0.80	0.30	0.40
SINSHP	2.00	1.00	1.00	1.00	2.00	1.00	1.00	2.00	2.00	2.00	2.00	1.00	1.00	1.50	1.00	1.00	1.00	1.00	1.00	1.00
PERI	32.0	17.0	37.0	20.0	28.0	21.0	43.0	16.0	25.0	30.0	26.0	22.0	21.0	26.0	28.0	94.0	18.0	45.0	39.0	23.0
PUBAD	0	1	3	2	0	0	2	99	0	3	2	1	1	3	2	1	2	0	0	4
PUBAB	3	4	4	3	2	99	5	5	2	5	4	2	4	4	4	99	4	3	1	1
LAT	64.52	69.42	65.30	69.25	63.00	65.50	60.43	61.00	99.00	64.50	63.25	64.08	65.56	62.12	64.23	55.53	66.37	70.00	64.32	64.32
LONG	147.50	141.31	138.15	145.10	150.00	128.00	135.03	144.00	99.00	147.51	149.30	141.20	137.24	131.47	138.21	134.15	149.19	160.00	163.45	163.45

CHARACTER	OTU																			
	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
SHAPE	1	2	1	1	2	1	2	2	2	1	2	1	2	1	2	2	2	2	1	2
MAXW	6.20	5.20	8.70	7.50	7.60	6.40	10.50	5.30	10.20	6.20	12.60	6.00	6.00	4.00	9.80	9.70	8.50	4.00	5.50	13.00
MAXL	4.40	2.00	6.00	6.60	5.80	5.40	9.20	3.80	8.30	6.00	13.60	5.50	5.50	3.20	7.20	7.30	6.50	3.00	4.90	10.40
APWID	5.0	4.5	10.0	6.5	5.1	6.6	8.1	4.7	10.0	6.5	15.0	6.4	6.6	3.9	9.0	9.2	6.4	3.4	5.2	10.6
APANGL	58	50	49	50	50	60	60	51	60	48	50	60	70	60	50	52	50	50	50	46
BAPANGL	20	60	40	20	34	30	75	90	50	60	70	30	55	45	28	50	80	50	50	70
NO1LB	6	8	10	8	9	10	10	8	11	8	7	5	8	9	6	7	10	7	10	9
NO2LB	1	6	25	15	5	2	9	7	18	8	9	8	9	5	4	9	10	5	2	10
LBAPSHP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	1.0	1.0	1.0	2.0	2.0	2.0	2.0
NOTETH	20	9	6	9	10	20	10	12	22	11	12	6	11	7	9	5	11	11	6	9
TETHSHP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	1.0	1.0	1.0	2.0	2.0	2.0	2.0
SINDEP	0.70	0.90	1.40	1.00	1.20	1.20	0.37	1.50	3.40	1.20	3.00	1.00	0.70	0.80	1.20	2.00	1.50	1.40	1.20	0.38
SINWID	0.70	0.80	0.60	0.90	0.70	0.80	0.90	0.50	0.60	0.70	2.40	0.80	0.90	0.40	1.00	0.80	0.90	0.30	0.50	1.40
SINSHP	1.00	2.00	1.00	1.00	1.50	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	1.00
PERI	28.0	22.0	48.0	36.0	34.0	30.0	67.0	22.0	60.0	31.0	58.0	28.0	24.0	22.0	37.0	48.0	30.0	23.0	24.0	65.0
PUBAD	1	99	4	2	2	1	0	2	0	0	0	0	0	1	4	2	0	2	0	1
PUBAB	4	4	2	4	5	5	3	4	4	99	2	99	99	2	99	99	4	99	4	99
LAT	61.26	69.18	68.41	66.34	67.25	52.45	99.00	59.45	99.00	60.22	68.40	67.58	67.58	56.00	58.00	99.00	61.37	60.00	67.25	99.00
LONG	165.27	145.04	141.13	164.25	150.07	179.18	99.00	127.20	99.00	133.51	134.07	133.41	133.41	129.00	134.00	99.00	133.03	137.00	139.46	99.00
	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
SHAPE	2	2	2	1	2	2	1	2	2	1	2	2	1	1	4	3	2	2	1	1
MAXW	10.00	8.00	6.70	4.20	6.60	3.50	3.10	6.80	7.90	9.20	3.50	9.20	6.70	6.90	8.40	3.50	4.50	6.70	5.90	5.40
MAXL	7.90	7.80	5.80	3.60	5.80	3.70	3.80	5.30	5.10	7.30	2.70	7.20	5.20	5.20	6.50	2.40	2.70	6.50	5.20	4.40
APWID	10.1	7.9	5.0	3.6	6.8	3.4	4.1	5.9	5.8	9.1	3.3	8.4	6.0	7.1	6.5	3.2	3.1	7.0	6.0	4.8
APANGL	53	40	61	40	50	43	54	60	55	60	50	53	60	32	71	60	70	55	60	40
BAPANGL	60	65	50	30	70	90	30	60	60	40	60	60	40	43	2	50	43	60	42	80
NO1LB	10	13	8	9	7	8	7	7	11	10	6	9	7	9	13	7	6	7	8	7
NO2LB	3	3	8	5	14	1	8	11	14	10	3	11	12	12	13	3	15	14	8	11
LBAPSHP	2.0	1.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	1.0	1.0	2.0	1.0	2.0	1.0	1.5	2.0	2.0	2.0	2.0
NOTETH	4	7	14	13	32	4	12	5	10	11	3	8	8	9	6	3	7	5	14	14
TETHSHP	2.0	1.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	1.0	1.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SINDEP	1.50	0.14	1.30	0.60	2.00	0.60	0.90	2.00	2.30	1.20	0.70	2.00	1.60	1.10	1.10	0.30	0.80	1.30	1.50	1.50
SINWID	0.90	0.80	0.40	0.60	0.50	0.50	0.80	0.50	0.50	0.70	0.10	1.50	0.40	0.60	1.20	0.30	0.40	0.70	0.80	0.50
SINSHP	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PERI	42.0	36.0	32.0	16.0	44.0	12.0	16.0	16.0	38.0	44.0	16.0	34.0	28.0	32.0	34.0	12.0	19.0	30.0	30.0	30.0
PUBAD	0	2	2	4	0	0	1	4	0	3	2	1	1	3	3	2	3	2	2	2
PUBAB	2	2	4	4	4	4	4	4	3	4	99	3	99	3	4	4	4	3	2	3
LAT	61.23	67.46	99.00	99.00	51.26	63.56	99.00	51.00	54.35	61.52	58.30	66.20	65.22	66.04	66.04	63.24	64.13	66.34	55.56	65.49
LONG	129.30	136.02	99.00	99.00	116.11	135.42	99.00	115.00	121.65	154.33	134.15	152.05	145.25	137.19	137.19	148.56	145.50	144.16	137.24	137.46

CHARACTER	OTU																			
	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
SHAPE	1	2	4	2	4	4	4	4	4	4	4	4	4	4	4	6	4	6	6	4
MAXW	4.00	8.70	6.30	13.20	9.40	15.40	18.30	12.80	8.90	9.20	9.70	13.00	8.50	19.80	18.80	9.20	15.00	16.40	6.50	8.50
MAXL	3.70	5.60	3.90	7.90	5.20	5.70	10.80	7.70	5.50	6.50	6.60	7.50	4.60	12.30	9.50	5.20	8.50	8.50	4.00	5.00
APWID	4.5	6.9	5.3	10.9	6.5	10.2	14.0	7.7	5.5	7.4	7.0	10.4	5.5	16.2	12.5	4.5	9.7	11.5	4.8	7.3
APANGL	50	60	60	61	70	67	62	64	58	50	55	61	79	73	57	51	57	70	55	60
BAPANGL	30	70	50	20	5	0	40	62	0	20	45	40	63	55	28	8	50	10	41	50
NO1LB	9	7	9	7	6	10	7	8	7	7	9	10	7	8	7	7	7	9	5	8
NO2LB	11	8	13	6	4	5	5	5	7	5	7	7	0	0	4	0	4	4	4	5
LBAPSHP	1.0	1.0	2.0	2.0	1.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
NOTETH	7	11	20	10	18	42	21	41	25	19	16	34	0	27	40	14	26	36	17	22
TETHSHP	1.0	1.0	2.0	2.0	1.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	99.0	2.0	2.0	3.0	2.0	2.0	2.0	2.0
SINDEP	1.00	0.70	2.50	4.00	3.10	4.70	4.00	5.60	4.50	3.00	2.70	4.40	3.40	8.90	6.80	2.90	0.85	0.68	3.40	3.00
SINWID	0.40	1.00	0.20	1.40	0.40	1.10	1.60	0.90	0.80	0.80	0.90	1.40	1.30	1.30	1.50	2.00	0.80	0.70	0.50	1.50
SINSHP	1.00	1.00	1.00	1.00	1.00	1.50	1.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PERI	26.0	28.0	44.0	74.0	66.0	118.0	87.0	88.0	82.0	47.0	47.0	75.0	43.0	120.0	138.0	45.0	90.0	102.0	38.0	39.0
PUBAD	1	0	1	1	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	0
PUBAB	99	99	1	99	2	99	1	99	1	2	0	1	1	1	1	0	1	1	1	1
LAT	99.00	68.06	57.65	43.00	99.00	47.20	51.00	53.00	54.10	49.00	68.13	37.10	48.30	50.20	46.00	47.00	45.30	45.40	52.17	58.12
LONG	99.00	165.46	122.35	124.90	99.00	123.00	116.00	122.00	125.20	123.00	135.53	121.40	88.00	93.10	89.00	91.00	87.30	85.00	77.20	62.40
	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
SHAPE	4	4	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
MAXW	13.00	16.60	13.80	11.20	11.00	16.60	4.00	19.30	10.80	8.90	12.00	8.10	14.80	5.60	5.90	9.70	6.50	6.00	6.90	7.90
MAXL	7.40	9.00	8.30	7.00	7.00	8.40	2.30	11.10	6.50	5.50	5.50	4.00	8.30	2.90	3.30	5.70	3.70	3.20	4.20	5.40
APWID	11.0	10.2	9.1	7.4	9.7	10.0	2.0	11.8	8.8	7.7	7.4	6.8	10.0	4.3	5.0	8.5	4.4	4.3	6.8	9.0
APANGL	70	77	52	30	74	68	60	74	70	60	57	77	70	60	57	68	59	56	58	52
BAPANGL	40	40	20	55	70	20	20	60	40	40	72	50	50	29	60	0	40	50	20	30
NO1LB	9	7	7	7	11	9	7	9	8	9	5	5	9	6	7	9	7	8	9	7
NO2LB	9	1	9	6	4	8	2	8	8	9	0	2	5	1	1	5	1	6	2	4
LBAPSHP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	1.0	2.0	2.0	3.0	2.0	2.0	2.0
NOTETH	11	26	10	10	27	26	9	32	30	13	2	31	22	0	24	23	6	12	22	23
TETHSHP	2.0	3.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	99.0	2.0	2.0	3.0	2.0	2.0	2.0
SINDEP	4.10	6.00	3.60	4.20	3.00	5.90	1.50	5.80	2.20	2.70	0.38	2.50	0.76	1.50	1.90	4.00	1.80	2.30	2.50	3.00
SINWID	1.10	1.50	2.10	1.00	1.00	0.40	0.70	1.10	0.40	0.50	1.80	1.60	0.40	0.80	0.30	0.40	0.70	0.50	0.70	0.90
SINSHP	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.50	1.00	1.50	1.50	2.00	1.50	1.00	1.00	1.00
PERI	74.0	93.0	80.0	90.0	80.0	112.0	22.0	134.0	70.0	56.0	43.0	36.0	100.0	25.0	27.0	53.0	49.0	31.0	36.0	46.0
PUBAD	0	1	0	0	0	99	1	1	1	99	0	1	0	0	1	1	0	0	0	1
PUBAB	99	1	1	99	0	1	1	99	99	0	1	1	1	1	2	1	1	1	1	1
LAT	65.04	51.00	56.33	56.27	68.00	48.35	49.00	99.00	43.00	99.00	52.15	53.54	54.00	54.08	54.09	58.43	60.00	60.00	55.35	57.49
LONG	123.39	93.00	126.25	124.53	136.00	86.15	84.00	99.00	81.00	99.00	76.23	122.45	115.00	122.41	122.41	123.40	128.32	128.32	128.50	129.57

CHARACTER	OTU																			
	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
SHAPE	4	1	4	4	4	4	4	4	1	2	5	2	1	5	5	5	5	5	5	5
MAXW	6.80	3.90	10.80	12.80	10.30	13.50	9.60	16.30	18.50	14.70	10.30	10.00	22.70	15.70	4.00	3.60	5.40	16.80	11.50	10.50
MAXL	4.00	2.00	5.70	7.40	5.50	9.20	5.20	9.50	11.00	10.50	6.80	6.50	17.00	12.20	4.00	3.10	3.30	13.30	8.50	8.20
APWID	5.5	2.9	5.1	7.9	6.0	8.0	5.7	14.0	15.0	14.3	9.7	1.0	20.7	16.3	4.1	4.3	4.6	17.3	8.7	8.2
APANGL	59	70	73	69	65	70	72	50	50	40	52	60	44	50	40	40	48	47	51	50
BAPANGL	20	0	20	30	30	78	50	0	0	40	20	0	40	40	40	50	50	0	35	60
NO1LB	8	8	9	9	8	7	9	9	7	9	14	13	11	7	10	10	8	9	8	9
NO2LB	4	2	4	6	7	0	5	10	6	0	8	0	4	5	3	5	0	2	0	0
LBAPSHP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	1.0	2.0
NOTETH	19	5	38	16	52	13	16	44	18	23	16	44	24	35	3	2	5	16	2	4
TETHSHP	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	1.0	2.0
SINDEP	2.80	0.90	4.00	4.00	4.00	0.63	3.00	5.60	5.30	2.50	1.30	1.90	4.50	2.20	0.80	2.00	1.00	3.50	2.40	2.00
SINWID	0.80	0.40	0.70	1.00	0.50	1.70	1.60	0.70	1.30	0.80	1.50	1.50	1.00	1.60	0.40	0.80	1.00	1.50	2.30	2.00
SINSHP	1.00	1.50	1.00	1.00	1.00	1.50	2.00	1.00	1.00	1.00	2.00	2.00	2.00	1.00	2.00	2.00	2.00	1.00	1.00	1.00
PERI	44.0	12.0	54.0	73.0	54.0	80.0	54.0	108.0	53.0	58.0	39.0	48.0	113.0	67.0	18.0	14.0	18.0	83.0	50.0	47.0
PUBAD	0	0	2	1	1	0	1	0	0	0	4	0	1	0	3	3	0	99	0	0
PUBAB	1	1	1	2	1	1	99	4	1	99	99	4	1	99	3	2	99	1	1	1
LAT	60.03	61.00	57.03	99.00	58.50	55.48	60.02	47.30	52.00	50.00	99.00	53.43	51.11	53.00	57.00	99.00	99.00	99.00	48.13	59.27
LONG	128.53	133.01	122.31	99.00	115.00	120.21	112.38	123.00	113.00	120.00	99.00	113.10	115.34	101.00	129.00	99.00	99.00	99.00	90.10	113.33
	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
SHAPE	5	5	5	5	5	5	5	5	5	5	5	5	5	1	2	5	5	5	4	1
MAXW	7.30	4.00	8.00	3.70	11.00	10.80	11.70	6.00	16.30	12.80	9.00	7.40	9.30	23.40	12.00	3.50	10.40	5.40	25.00	9.20
MAXL	5.00	3.20	5.50	3.70	7.00	7.00	7.70	4.00	13.50	8.30	8.00	4.80	4.80	16.80	9.50	1.90	6.00	3.40	11.50	8.20
APWID	6.6	3.6	8.2	4.8	9.2	9.2	12.0	4.6	16.2	11.0	11.2	7.0	5.0	23.3	11.5	2.7	10.5	4.9	16.0	10.8
APANGL	50	45	56	40	45	51	90	60	36	45	40	52	42	56	57	30	77	62	50	40
BAPANGL	30	60	26	40	24	27	20	0	50	52	35	0	60	32	30	69	20	10	10	30
NO1LB	9	6	7	7	8	12	11	9	9	7	7	7	8	8	8	7	10	7	9	10
NO2LB	1	0	5	0	3	0	11	3	2	3	3	0	5	10	2	4	3	0	3	1
LBAPSHP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.5	2.0	2.0
NOTETH	8	2	19	7	10	17	15	4	17	17	30	17	21	26	27	4	11	0	33	6
TETHSHP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	0.0	2.0	2.0
SINDEP	1.30	1.00	1.80	0.90	2.40	2.40	2.40	1.00	5.10	2.70	2.50	1.50	1.90	6.70	3.30	0.40	2.60	1.80	4.80	1.50
SINWID	1.00	1.00	1.20	1.20	1.50	2.30	1.50	0.60	1.40	1.30	1.30	0.80	1.00	1.00	0.70	0.50	7.00	0.90	0.50	1.90
SINSHP	1.00	1.00	2.00	1.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	2.00	1.00	1.00	1.50	2.00	1.00	1.00	1.00
PERI	35.0	16.0	36.0	19.0	43.0	50.0	59.0	22.0	102.0	56.0	54.0	30.0	34.0	146.0	66.0	9.0	60.0	26.0	100.0	36.0
PUBAD	2	0	0	3	99	0	1	0	1	1	2	3	0	1	0	0	0	0	1	0
PUBAB	99	0	1	99	4	1	2	99	1	2	3	99	5	4	1	3	5	5	1	4
LAT	60.00	49.51	99.00	51.00	58.51	52.37	53.00	59.22	54.36	50.00	49.52	50.32	52.37	54.42	54.42	55.10	58.46	54.68	55.46	53.36
LONG	112.22	95.33	99.00	115.00	113.56	103.56	114.00	63.48	97.50	100.00	99.22	99.57	103.56	117.17	117.17	118.50	120.21	125.21	120.21	118.19

CHARACTER	OTU																			
	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
SHAPE	1	1	1	1	5	2	1	2	5	5	5	1	1	5	5	1	1	4	1	2
MAXW	6.70	15.20	9.10	15.00	19.20	18.60	25.50	13.00	10.90	20.70	9.00	11.40	8.80	9.80	18.50	12.10	10.80	10.00	9.90	14.50
MAXL	4.70	11.20	6.50	11.00	12.50	11.00	24.00	10.90	6.40	12.70	6.60	10.50	8.30	8.50	16.00	14.70	11.40	9.50	9.80	13.70
APWD	7.3	16.2	8.0	14.3	17.7	13.4	32.0	11.5	7.2	15.0	8.0	12.5	8.0	11.0	15.5	17.7	13.0	7.7	10.0	13.0
APANGL	50	50	51	47	53	54	51	50	65	58	46	50	50	40	85	31	40	68	40	48
BAPANGL	40	40	20	30	60	60	50	60	45	30	40	40	25	25	55	64	50	40	60	70
NO1LB	8	9	6	12	8	9	9	6	11	9	4	5	12	11	10	0	0	0	0	0
NO2LOB	5	2	0	5	0	0	4	3	0	0	0	0	11	8	3	0	0	0	0	0
LBAPSHP	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	0.0	0.0	0.0	0.0	0.0
NOTETH	9	6	16	25	4	17	21	16	20	23	12	18	34	6	17	15	27	41	32	46
TETHSHP	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0
SINDEP	1.00	2.50	1.50	2.70	4.20	3.70	6.90	3.30	2.00	4.50	1.80	1.00	1.50	1.70	2.40	0.00	0.00	0.00	0.00	0.00
SINWID	0.60	2.60	0.80	2.20	2.40	2.00	1.10	2.50	2.20	1.50	0.90	1.00	0.30	1.20	1.50	0.00	0.00	0.00	0.00	0.00
SINSHP	1.00	1.00	1.00	1.00	2.00	2.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	1.00	2.00	0.00	0.00	0.00	0.00	0.00
PERI	26.0	53.0	38.0	80.0	90.0	84.0	160.0	60.0	44.0	90.0	52.0	46.0	50.0	40.0	28.0	56.0	39.0	44.0	36.0	49.0
PUBAD	0	0	1	2	0	0	0	0	0	0	1	99	0	4	4	1	4	4	0	1
PUBAB	99	1	3	4	99	1	4	99	99	2	1	2	4	3	99	99	2	5	5	99
LAT	58.50	52.00	51.11	51.05	57.00	52.51	99.00	56.00	49.39	49.00	51.11	64.05	52.45	51.06	99.00	61.00	99.00	60.44	64.29	64.13
LONG	115.00	113.00	114.30	115.30	92.00	104.03	99.00	120.00	110.18	113.00	114.30	139.25	125.15	123.00	99.00	147.00	99.00	143.34	148.45	145.49

	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
SHAPE	1	1	1	1	1	1	1	1	1	1	1	5	1	1	1	1	1	1	1	1
MAXW	10.00	13.30	11.20	16.00	7.50	7.80	10.70	9.00	6.30	5.50	3.00	10.20	11.00	14.40	8.70	7.00	6.00	14.20	4.70	4.70
MAXL	10.20	15.80	11.60	12.00	9.00	9.50	9.80	11.50	6.60	6.70	3.50	7.80	13.80	14.50	9.10	8.70	6.00	13.00	5.70	7.90
APWD	12.0	17.0	13.4	16.5	10.8	14.4	15.0	11.4	9.5	8.6	4.0	99.0	15.0	16.5	9.3	7.0	6.5	15.0	7.3	8.9
APANGL	53	55	54	60	40	42	35	40	35	40	31	53	45	45	60	60	42	48	45	28
BAPANGL	30	60	5	30	55	18	30	70	50	30	60	20	60	33	35	40	49	60	30	35
NO1LB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NO2LOB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LBAPSHP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOTETH	38	51	44	42	38	36	20	43	35	50	0	0	40	44	33	30	26	46	25	26
TETHSHP	3.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	2.0	2.0	0.0	0.0	2.0	1.0	1.0	2.0	3.0	2.0	2.0	3.0
SINDEP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SINWID	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SINSHP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PERI	41.0	56.0	42.0	60.0	29.0	40.0	48.0	36.0	26.0	30.0	12.0	38.0	45.0	65.0	58.0	35.0	28.0	49.0	18.0	26.0
PUBAD	1	2	1	1	2	4	4	2	99	99	4	2	2	2	0	0	99	3	99	99
PUBAB	99	99	3	4	5	4	99	99	5	5	5	4	4	99	2	5	3	4	5	5
LAT	61.15	64.53	63.07	48.00	55.41	51.30	99.00	50.00	51.37	49.00	53.40	99.00	68.12	49.00	61.15	58.43	56.15	57.00	99.00	50.00
LONG	134.44	147.51	142.40	121.00	124.30	120.46	99.00	133.00	123.25	115.00	113.20	99.00	135.00	115.00	138.44	122.44	120.50	129.00	99.00	99.00

CHARACTER	OTU																			
	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261
SHAPE	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1
MAXW	9.20	9.50	18.40	6.10	6.10	9.60	1.50	11.60	8.20	12.70	8.20	11.90	19.60	3.00	9.10	17.00	9.50	7.40	5.00	6.00
MAXL	12.50	9.50	16.20	8.70	8.00	10.70	3.00	9.60	8.00	13.00	8.20	8.00	19.00	3.20	7.70	11.30	8.50	7.10	6.30	7.80
APWID	13.8	12.2	22.5	11.7	8.5	11.2	4.0	10.3	7.8	17.5	9.1	10.8	26.5	3.3	10.1	15.4	10.8	7.0	7.3	10.2
APANGL	35	40	52	50	75	32	28	60	52	50	40	48	48	36	50	53	51	53	30	42
BAPANGL	42	40	10	42	35	70	0	60	50	50	70	52	0	50	30	60	30	79	40	38
NO1LB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NO2LOB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LBAPSHP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOTETH	58	42	38	32	28	38	0	27	28	43	38	46	56	32	25	26	43	22	37	49
TETHSHP	2.0	2.0	1.0	3.0	2.0	2.0	0.0	1.0	3.0	2.0	2.0	2.0	2.0	1.0	1.0	2.0	2.0	2.0	2.0	2.0
SINDEP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SINWID	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SINSHP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PERI	42.0	42.0	73.0	34.0	37.0	42.0	12.0	41.0	30.0	34.0	32.0	37.0	88.0	12.0	34.0	30.0	38.0	23.0	22.0	36.0
PUBAD	4	4	3	99	4	99	0	4	2	2	0	4	3	4	4	4	4	0	2	3
PUBAB	5	5	5	5	5	5	99	5	4	4	4	4	99	5	5	5	5	4	99	99
LAT	99.00	99.00	45.30	45.00	47.00	43.00	54.46	47.00	99.00	49.00	58.43	60.00	50.15	57.05	54.00	57.00	42.00	99.00	49.53	58.47
LONG	99.00	99.00	112.00	93.00	86.00	123.00	115.00	91.00	99.00	109.00	94.05	110.12	99.50	122.35	110.00	92.18	105.00	99.00	97.09	94.11

	241	262	263	264	265	266	267	268	269	270	271
SHAPE	1	2	1	1	1	1	1	1	1	1	1
MAXW	4.00	7.00	4.60	5.40	5.00	9.10	12.00	8.00	4.20	3.50	7.10
MAXL	3.70	6.50	6.40	6.30	6.20	9.40	11.20	7.00	5.00	4.80	9.80
APWID	4.6	6.7	7.5	7.5	7.6	10.0	13.0	8.6	4.7	6.0	10.5
APANGL	35	38	30	40	40	60	60	64	35	31	38
BAPANGL	40	30	40	40	40	0	40	0	40	30	60
NO1LB	0	0	0	0	0	0	0	0	0	0	0
NO2LOB	0	0	0	0	0	0	0	0	0	0	0
LBAPSHP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOTETH	21	18	0	31	26	43	47	38	22	26	38
TETHSHP	2.0	1.0	0.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0
SINDEP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SINWID	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SINSHP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PERI	14.0	50.0	22.0	22.0	20.0	38.0	46.0	32.0	16.0	17.0	30.0
PUBAD	4	2	2	4	4	1	4	4	4	4	3
PUBAB	5	4	5	5	5	5	5	4	5	5	5
LAT	57.38	62.11	62.11	63.20	62.04	53.50	56.46	53.00	54.20	55.04	58.50
LONG	94.05	133.46	133.46	142.52	132.19	110.32	109.28	118.06	109.28	117.17	125.11

APPENDIX TWO: DATA MATRIX FOR MORPHOMETRIC ANALYSES OF STAMINATE CHARACTERS

MISSING DATA IS REPRESENTED BY 99, 99.0, OR 99.00.

CHARACTER	OTU																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
NOHEADS	8	7	7	7	5	5	3	5	13	6	12	8	12	9	8	4	8	6	8	5
PHYLWI	2.83	3.50	2.62	2.83	1.67	3.25	2.17	2.00	1.83	1.67	2.17	2.50	2.50	1.25	2.08	1.67	1.90	1.25	1.42	2.08
PHYLLEN	8.67	7.50	7.50	7.50	5.83	7.50	4.25	8.67	8.67	7.25	9.17	8.58	7.92	7.92	7.25	6.67	7.90	5.83	7.25	6.83
PHYLMAR	2.5	2.5	2.0	2.0	2.0	2.0	2.0	2.5	2.5	2.0	2.5	2.0	2.0	2.5	2.0	2.5	2.0	2.5	2.5	2.5
NORF	7	8	7	10	6	6	9	10	5	8	9	8	10	12	5	10	8	8	9	9
POSRF	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
RL	4.17	4.58	2.67	4.83	5.58	4.58	5.00	5.42	4.67	4.42	6.08	3.75	5.75	6.00	7.17	3.92	3.83	5.67	3.17	6.25
RW	2.50	2.08	1.08	1.20	1.67	2.67	1.17	1.83	1.17	1.50	1.42	0.83	1.67	1.50	1.98	2.02	1.12	0.92	1.28	1.83
STYLEN	6.58	7.50	4.42	5.67	9.83	5.40	7.42	9.50	6.67	6.08	6.25	4.58	7.92	8.08	4.58	6.67	7.67	6.50	5.33	4.50
LENSTBR	0.30	0.30	0.36	0.30	0.14	0.30	0.28	0.24	0.10	0.10	0.26	0.28	0.28	0.40	0.20	0.30	0.42	0.40	0.20	0.26
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	5.00	2.92	2.67	3.50	4.17	4.40	2.50	6.00	3.08	2.33	2.92	2.08	4.33	7.08	1.90	3.30	4.58	4.83	2.17	3.75
NOOF	35	43	49	34	43	38	42	38	39	32	54	35	41	30	18	29	36	32	27	22
POSDF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
CORLEN	3.75	4.00	3.92	3.67	4.75	4.17	4.17	4.58	4.08	3.83	3.38	3.75	4.17	3.20	3.75	3.80	4.25	3.80	3.32	3.30
CORLBWI	0.72	0.92	0.76	0.68	1.08	0.76	0.44	1.00	0.52	0.67	0.40	0.64	0.83	0.60	0.58	0.44	0.64	0.48	0.40	0.60
STYLENG	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
LENGSTBR	9.67	5.42	10.50	8.83	12.67	9.17	10.17	12.33	9.50	10.00	8.33	7.92	10.50	10.83	9.33	10.00	9.50	8.83	9.00	10.17
STYLTEX	0.76	1.04	1.00	0.96	1.00	0.80	1.10	0.84	1.32	1.10	0.80	1.00	2.00	0.90	0.88	1.00	1.24	0.84	0.76	0.80
LENANTH	2.0	2.0	2.0	2.0	2.0	2.0	1.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPANAPP	1.60	1.83	1.92	1.84	2.20	2.00	1.84	1.92	2.40	1.80	2.08	2.08	2.32	1.52	1.88	1.60	2.08	1.80	1.72	1.60
SHPCORLB	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
PAPLENDF	3.75	3.50	4.00	3.50	6.17	3.98	2.33	6.25	4.17	2.17	4.75	3.75	5.00	4.42	1.41	5.00	4.08	5.25	3.83	6.33
DCLL	1.60	2.08	1.76	1.88	2.30	1.24	1.64	1.58	1.80	1.66	1.60	1.60	1.82	1.48	1.84	1.40	1.80	2.00	1.40	1.16
LAT	63.23	66.38	64.52	99.00	63.00	63.47	52.00	60.23	62.11	63.54	64.50	63.37	62.22	60.31	60.42	59.56	99.00	66.54	99.00	99.22
LONG	143.53	148.34	147.52	99.00	149.00	171.45	174.00	166.11	131.47	142.15	147.51	148.35	145.15	127.52	137.34	141.42	99.00	164.37	99.00	152.06
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
NOHEADS	10	7	8	6	3	4	6	8	5	4	8	4	7	5	5	3	9	6	12	11
PHYLWI	1.25	2.75	1.80	2.50	2.04	1.83	2.08	1.50	1.08	3.08	2.42	3.17	1.00	2.17	2.75	1.67	2.50	4.41	1.50	2.67
PHYLLEN	9.20	8.70	7.90	5.91	7.50	9.17	8.50	5.42	7.75	7.92	8.33	6.50	6.50	8.08	7.33	6.83	7.50	7.33	8.08	8.33
PHYLMAR	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.5	2.0	2.0	2.5	2.5	2.0	2.0	2.5	2.5	2.0	2.0	2.0	2.5
NORF	7	7	11	5	11	6	8	5	5	8	1	6	13	6	5	7	10	9	5	5
POSRF	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.5	1.0	1.0	1.0
RL	5.00	4.00	8.20	4.12	5.83	5.25	4.67	3.75	5.17	8.17	4.83	4.17	4.92	5.24	6.08	5.83	4.75	5.00	3.42	7.58
RW	1.25	1.70	2.00	1.75	2.08	2.42	1.00	1.58	1.50	3.75	3.42	1.67	3.00	1.80	2.33	1.58	1.67	3.33	1.40	1.67
STYLEN	7.10	7.50	8.80	6.50	7.67	6.67	6.67	5.67	8.67	10.67	7.67	5.33	7.00	6.08	7.08	5.83	7.92	8.00	5.25	7.08
LENSTBR	1.50	0.16	0.30	0.40	0.14	0.30	0.20	0.24	0.28	0.38	0.28	0.20	0.20	0.30	0.26	0.22	0.10	0.24	0.30	0.20
STYTEX	1.0	1.0	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	5.80	3.25	3.75	3.50	4.58	4.17	3.30	4.58	4.42	4.42	4.58	2.88	5.08	4.17	3.58	3.33	3.91	5.42	1.67	3.50
NOOF	27	25	38	33	30	20	43	28	40	25	23	78	44	23	33	19	47	44	23	34
POSDF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
CORLEN	3.60	4.20	5.10	3.25	4.75	4.17	3.83	3.33	3.00	4.83	4.08	3.48	4.25	4.17	3.40	3.24	4.25	4.12	3.42	3.80
CORLBWI	1.25	0.80	0.72	0.68	0.83	0.88	0.56	0.83	0.64	0.80	0.60	0.88	0.60	0.48	0.80	0.40	0.83	0.83	0.52	0.92
STYLENG	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
LENGSTBR	10.10	9.50	15.80	8.00	10.83	8.67	9.17	8.33	9.17	13.17	12.17	3.00	8.33	10.17	11.00	8.83	11.50	9.80	8.17	10.00
STYLTEX	1.00	0.80	0.06	1.40	1.18	1.16	1.40	0.68	0.98	1.04	1.24	1.52	1.24	1.12	1.20	0.80	1.22	1.00	1.00	0.80
LENANTH	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPANAPP	1.90	1.80	2.20	1.68	2.48	1.82	1.52	0.52	1.92	2.36	2.64	1.48	1.52	2.00	1.72	1.78	2.00	1.60	1.80	1.64
SHPCORLB	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	3	2	2
PAPLENDF	5.40	4.60	5.80	3.75	4.00	3.75	3.50	4.75	4.83	4.58	3.30	2.92	4.17	4.17	5.20	5.00	4.33	4.58	1.92	5.33
DCLL	2.02	0.80	1.90	1.60	2.58	0.84	1.48	1.25	1.52	2.00	1.42	1.84	1.92	1.48	1.32	1.76	1.84	1.50	1.48	1.76
LAT	68.14	56.00	63.22	99.00	99.00	61.37	60.25	71.08	63.58	99.00	65.11	57.13	61.32	71.20	70.08	69.50	51.45	61.55	62.07	64.23
LONG	134.50	128.00	126.42	99.00	99.00	141.58	172.36	157.02	135.42	99.00	123.28	133.27	166.05	156.39	158.42	155.30	178.45	165.50	131.53	138.21

CHARACTER	OTU																			
	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
NOHEADS	5	9	8	9	9	7	12	10	7	20	10	7	5	6	7	7	7	10	7	8
PHYLWI	3.33	2.67	1.67	3.30	2.67	1.67	1.58	2.33	3.33	2.17	2.25	1.20	2.40	1.70	1.83	3.30	1.67	2.50	2.25	1.75
PHYLLEN	10.67	5.92	7.92	8.30	9.33	7.00	5.58	6.67	8.08	7.08	7.70	6.90	9.20	6.70	8.20	7.50	6.67	8.33	9.00	8.25
PHYLMAR	2.5	2.0	2.0	2.0	2.5	2.5	2.0	2.0	2.0	2.5	2.0	2.0	2.5	2.0	1.0	1.0	2.0	2.0	2.0	2.0
NORF	8	13	7	5	8	5	8	11	7	12	10	6	3	7	3	8	11	6	7	10
POSRF	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	2.0	1.0	1.0
RL	6.25	5.00	4.17	5.42	5.00	8.33	3.00	3.33	5.42	2.75	5.00	3.40	6.70	5.00	4.50	4.90	3.50	4.58	4.17	6.08
RW	1.50	1.08	1.67	2.50	1.17	3.75	1.20	1.25	2.75	0.30	2.50	0.28	1.30	2.50	0.10	2.30	0.88	2.67	1.58	1.42
STYLEN	9.83	5.83	5.83	6.67	7.50	8.00	6.75	6.25	7.50	7.00	8.50	6.90	7.50	6.80	8.75	2.75	5.25	8.08	7.58	7.50
LENSTBR	0.68	0.24	0.38	0.16	0.26	0.32	0.60	0.22	0.24	0.44	0.24	0.40	0.28	0.28	0.36	0.20	0.28	0.40	0.40	0.24
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	6.33	4.17	2.92	4.58	1.67	7.50	2.08	2.17	5.42	2.75	2.80	2.70	4.20	2.70	3.75	4.80	3.75	2.08	1.83	2.92
NOOF	47	46	18	26	37	24	38	27	39	46	38	33	68	26	22	40	47	28	39	41
POSDF	1.5	1.5	1.5	1.5	1.5	1.5	2.0	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
CORLEN	4.42	3.58	2.44	4.17	4.17	4.42	2.92	3.30	4.00	3.30	4.00	3.75	4.30	4.20	3.30	4.40	3.44	3.32	4.33	4.00
CORLBWI	0.60	0.60	0.64	1.08	0.67	0.40	0.80	0.80	0.48	0.32	0.64	0.44	1.58	0.50	0.50	0.72	0.64	0.92	1.00	0.48
STYLENG	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
LENGSTBR	11.67	9.17	8.33	9.17	10.83	8.08	7.42	7.33	11.50	10.17	9.20	9.50	10.80	10.30	12.50	4.50	7.25	8.83	13.00	8.33
STYLTEX	0.50	1.00	1.60	1.08	0.88	0.80	0.80	0.88	0.60	0.60	1.04	0.44	1.00	0.68	0.05	0.84	0.80	1.04	0.80	0.72
LENANTH	2.0	2.0	2.0	2.0	1.0	2.0	2.0	3.0	2.0	1.5	2.0	2.0	1.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPANAPP	2.24	1.40	1.84	2.00	1.88	2.00	1.64	2.00	1.72	2.24	1.88	2.30	2.20	2.70	2.00	2.00	1.92	1.92	2.44	2.60
SHPCORLB	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
PAPLENDF	5.00	3.75	4.00	6.08	3.75	8.50	3.30	2.75	5.83	4.17	4.90	5.00	5.40	3.30	5.00	4.75	3.30	3.90	4.17	4.83
DCLL	1.60	1.25	1.60	1.17	1.67	0.83	1.44	1.00	1.72	2.00	1.67	1.90	2.04	1.48	1.60	1.42	1.40	1.68	2.00	1.64
LAT	64.08	64.18	99.00	99.18	58.48	44.00	60.45	99.00	99.00	99.00	58.00	49.00	54.40	51.20	56.00	60.58	50.00	50.31	61.10	61.00
LONG	141.20	148.42	99.00	145.04	134.33	138.22	147.00	99.00	99.00	99.00	129.00	122.00	127.30	116.13	120.00	136.35	122.00	123.10	145.40	137.00
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
NOHEADS	15	8	5	6	6	6	4	6	7	6	7	7	11	4	2	16	9	18	26	32
PHYLWI	2.00	2.25	1.80	2.92	1.58	2.33	2.08	1.84	2.50	2.08	2.50	1.67	2.08	2.58	2.17	2.00	3.67	1.82	2.42	2.50
PHYLLEN	8.33	7.50	3.64	7.08	6.25	7.92	7.50	7.50	8.92	7.25	10.00	7.83	7.00	8.17	8.67	6.83	12.80	9.50	10.00	11.00
PHYLMAR	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.5	2.5	2.0	2.5	2.5	2.0	2.5	1.0	1.0	1.0	1.0
NORF	9	9	8	8	8	8	6	9	7	8	7	7	8	6	2	9	11	12	12	24
POSRF	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	2.0	1.0	1.0	1.0	1.0	1.0
RL	6.42	3.50	7.42	5.00	4.83	3.58	5.58	4.58	4.67	7.08	5.00	4.67	5.08	12.00	1.60	4.08	5.67	5.50	3.00	3.90
RW	1.75	1.25	2.08	1.25	1.67	0.64	1.67	1.25	1.75	2.50	0.83	1.50	1.25	1.28	0.48	1.40	0.84	0.72	0.72	1.00
STYLEN	8.83	8.83	8.67	7.67	8.67	7.08	7.92	5.83	7.17	8.00	7.67	6.25	7.50	8.50	8.33	6.25	8.91	7.50	8.67	7.50
LENSTBR	0.34	0.34	0.54	0.24	0.30	0.24	0.16	0.14	0.30	0.36	0.36	0.16	0.18	0.16	0.80	0.10	0.28	0.22	0.28	0.20
STYTEX	1.0	1.0	1.0	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	4.83	1.75	2.25	3.75	4.00	3.58	4.00	3.00	2.92	4.33	4.17	2.00	2.17	5.50	4.67	3.67	9.42	3.00	3.67	4.17
NOOF	32	34	28	28	32	28	34	41	36	25	31	35	23	34	50	24	38	43	28	55
POSDF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	2.0	1.5	1.5	2.0
CORLEN	4.17	3.83	6.08	3.60	3.02	3.40	4.42	3.24	3.28	4.25	4.83	4.17	3.16	5.25	4.17	4.17	4.08	3.58	3.92	3.83
CORLBWI	0.60	0.80	0.84	0.56	0.64	0.80	1.25	0.40	0.52	0.72	1.00	0.88	0.40	0.52	4.00	0.80	0.56	0.40	0.56	0.48
STYLENG	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
LENGSTBR	10.17	10.33	13.67	8.33	10.00	9.50	11.83	6.67	8.00	13.17	11.50	8.67	10.83	13.30	11.50	8.83	10.00	7.75	9.12	10.50
STYLTEX	1.32	1.40	1.24	1.20	1.24	0.80	0.88	1.12	0.80	1.20	1.33	0.92	1.00	0.80	1.10	0.80	0.32	0.28	0.42	0.24
LENANTH	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.5	2.0	2.0	2.0	2.0	2.0	2.0	1.5	1.0	1.0	1.0	1.5
SHPANAPP	2.48	2.08	2.24	1.60	1.88	1.76	1.84	1.36	1.82	2.08	2.02	1.84	1.88	2.36	2.12	2.40	2.20	2.00	1.80	1.82
SHPCORLB	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
PAPLENDF	5.50	3.58	3.08	4.17	8.08	3.75	5.00	4.00	4.17	5.42	5.00	3.92	2.50	8.62	8.25	4.17	5.50	3.82	5.42	4.42
DCLL	2.08	1.67	2.24	1.60	1.64	1.36	1.88	1.08	1.88	1.48	1.82	1.48	1.00	1.48	1.67	2.08	2.88	0.85	3.08	2.48
LAT	52.10	51.00	61.10	99.00	50.00	99.00	60.96	58.10	57.47	65.48	52.40	62.00	63.53	99.41	60.58	58.56	43.00	44.00	47.30	48.00
LONG	117.20	116.00	132.59	99.00	122.00	99.00	134.52	154.96	152.24	137.46	118.15	132.00	134.30	141.13	145.00	128.18	124.00	123.00	123.30	124.00

CHARACTER	OTU																			
	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
NOHEADS	15	16	8	27	14	7	10	8	13	15	12	24	24	8	15	8	11	4	10	17
PHYLWI	2.50	2.50	1.83	1.92	1.67	2.25	3.30	2.00	1.83	2.17	2.17	2.50	2.00	2.08	1.60	2.75	2.67	1.75	2.36	1.67
PHYLLEN	8.33	8.83	7.25	10.50	8.58	10.50	5.80	5.80	7.67	6.67	7.83	7.33	8.25	7.83	6.67	8.50	7.42	6.08	8.08	7.62
PHYLMAR	1.0	1.0	2.0	1.0	2.0	1.0	2.5	1.0	2.0	2.0	2.5	2.5	2.5	2.5	2.5	2.0	1.0	2.5	2.5	1.0
NORF	10	18	18	20	13	20	70	13	23	20	12	40	16	14	7	9	23	5	22	9
POSRF	1.0	1.0	1.0	1.0	1.0	1.0	1.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
RL	4.42	4.58	5.33	5.42	5.33	4.40	2.90	5.20	3.75	3.58	4.00	5.08	5.00	4.67	5.17	5.00	6.25	3.50	6.33	5.41
RW	0.80	2.17	1.00	0.83	1.67	1.08	0.40	0.50	0.60	1.33	1.20	1.42	0.75	1.32	1.20	0.88	1.00	1.04	1.38	5.00
STYLEN	6.42	6.50	4.58	6.25	8.50	6.90	5.50	1.50	5.00	7.08	8.67	7.25	5.17	6.00	6.67	6.00	7.92	5.33	8.33	6.50
LENSTBR	0.26	0.18	0.20	0.16	0.24	0.32	0.12	0.30	0.20	0.08	0.20	0.26	0.12	0.24	0.36	0.28	0.20	0.18	0.10	0.10
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	4.42	3.58	2.92	3.33	5.00	5.40	2.40	5.00	2.50	5.00	3.75	3.92	3.75	3.08	4.17	5.00	4.00	4.58	6.25	3.33
NODF	37	50	38	54	22	47	11	31	28	15	27	14	37	27	20	22	33	15	22	30
POSDF	1.5	1.5	1.5	2.0	1.5	1.5	2.0	2.0	1.5	1.5	1.5	1.5	1.0	1.5	1.5	1.5	1.5	1.5	1.5	1.5
CORLEN	3.58	3.58	3.67	3.75	4.17	3.50	3.12	3.80	3.88	3.75	4.33	3.62	3.75	3.91	4.17	3.56	3.24	3.56	3.40	3.42
CORLBWI	0.63	0.60	0.67	0.60	0.40	0.50	0.72	0.58	0.52	0.56	0.44	0.48	1.00	0.68	0.72	0.75	0.60	0.76	0.60	0.40
STYLENG	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
LENGSTBR	9.67	8.25	8.67	7.75	10.80	7.17	5.70	23.00	9.50	9.17	8.33	7.75	8.67	10.00	8.33	9.50	9.83	7.25	10.67	7.92
STYLTEX	0.30	0.20	0.56	0.20	0.40	0.32	0.60	0.01	0.84	0.40	0.84	1.00	1.67	1.20	1.20	0.70	1.10	0.38	0.60	0.22
LENANTH	1.0	1.0	2.0	1.0	2.0	1.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	1.5	2.0	1.5	1.5	2.0	1.0
SHPANAPP	1.60	1.83	2.08	2.08	2.44	2.16	0.88	0.04	2.00	2.38	2.20	2.67	2.44	2.17	2.58	4.16	1.92	2.00	2.08	1.80
SHPCORLB	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
PAPLENDF	4.58	4.17	3.28	3.75	5.00	8.30	2.60	8.25	2.67	4.17	4.17	4.42	4.58	3.92	3.75	4.58	5.00	5.17	4.17	4.17
DCLL	2.17	0.72	1.50	1.40	2.24	2.75	1.24	1.58	2.20	1.72	2.04	3.04	1.92	1.80	2.68	2.58	1.56	1.68	2.00	2.42
LAT	99.00	47.00	57.00	49.43	54.33	43.00	52.00	49.00	99.00	99.00	42.58	50.15	48.26	51.00	53.30	45.00	37.06	57.50	99.00	47.30
LONG	99.00	123.40	128.05	124.30	127.23	124.00	118.00	123.00	99.00	99.00	81.14	93.15	89.13	115.00	84.32	83.22	121.58	99.00	99.00	123.30
	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
NOHEADS	14	24	27	10	8	12	15	22	32	10	16	21	19	13	17	9	6	7	3	7
PHYLWI	1.83	2.33	1.83	1.58	2.50	2.33	1.75	2.00	2.50	2.50	2.50	2.17	2.25	2.75	1.67	1.50	2.33	2.25	2.17	2.17
PHYLLEN	6.25	8.33	6.33	8.33	6.75	6.67	7.00	5.67	6.83	7.50	6.67	6.83	7.50	10.00	9.17	7.00	10.33	7.50	10.00	7.08
PHYLMAR	2.5	1.0	1.0	2.5	1.0	2.5	2.5	2.0	2.5	2.5	2.5	2.5	1.0	1.0	2.5	2.5	2.5	2.5	2.5	2.0
NORF	18	15	15	6	5	12	11	12	14	13	27	13	11	11	9	13	7	2	11	15
POSRF	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
RL	2.75	4.00	2.75	4.58	0.00	3.58	5.92	2.83	4.33	6.08	1.67	5.25	2.20	5.83	5.67	3.00	7.83	4.50	7.67	4.33
RW	1.17	0.83	0.58	1.67	0.00	1.83	1.00	1.00	0.83	2.50	0.40	1.33	0.88	0.92	0.83	1.00	1.75	1.67	2.02	3.50
STYLEN	4.58	6.83	7.08	6.00	6.67	5.00	6.83	5.67	6.00	7.50	7.42	6.58	5.83	10.33	6.75	5.50	8.50	5.83	8.83	5.00
LENSTBR	0.10	0.12	0.28	0.22	0.14	0.20	0.20	0.00	0.20	0.32	0.10	0.16	0.22	0.14	0.24	0.30	0.38	0.24	0.18	0.20
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	1.92	2.66	5.83	5.00	3.50	2.50	4.17	4.33	2.50	2.50	5.67	4.67	3.17	3.33	5.42	5.50	4.17	4.00	4.30	3.33
NODF	29	60	32	31	38	29	25	34	47	41	26	47	34	31	31	23	23	23	32	27
POSDF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	2.0	1.5	1.5
CORLEN	3.12	2.92	3.75	3.42	2.64	3.60	3.75	4.17	3.60	3.67	4.58	4.50	3.33	4.83	4.50	3.75	4.58	4.08	9.80	3.28
CORLBWI	0.58	0.52	0.75	0.48	0.68	0.68	0.90	0.66	0.60	1.00	0.80	0.68	0.56	0.68	0.32	0.80	0.78	0.58	0.60	0.64
STYLENG	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
LENGSTBR	7.50	8.33	10.33	7.58	8.33	7.50	9.83	7.50	7.25	10.00	10.33	11.50	7.75	11.33	10.00	7.08	11.80	9.67	10.30	5.67
STYLTEX	0.44	0.10	0.20	0.72	0.44	0.48	0.90	0.86	0.88	1.20	0.60	1.52	0.24	0.20	1.00	0.80	0.92	1.40	0.50	0.44
LENANTH	2.0	1.0	1.0	2.0	1.0	1.5	2.0	2.0	2.0	2.0	2.0	2.0	1.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPANAPP	2.24	1.72	1.76	2.20	1.40	2.20	2.36	2.25	2.38	1.68	2.52	2.40	1.84	2.00	2.44	1.96	2.40	2.08	2.24	1.92
SHPCORLB	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
PAPLENDF	3.92	4.50	5.83	3.75	3.08	4.58	4.00	4.58	1.92	3.75	6.08	5.83	4.83	4.58	4.58	5.80	5.42	5.17	5.58	3.30
DCLL	1.40	2.40	2.75	1.42	1.20	2.20	2.25	2.50	0.80	1.80	2.60	2.20	2.28	3.80	3.00	1.00	1.80	1.80	2.00	1.64
LAT	44.55	46.00	44.30	57.03	65.48	61.00	60.03	57.49	53.33	53.00	53.00	50.52	99.00	50.00	99.00	71.00	60.00	70.40	60.58	58.00
LONG	68.41	123.40	123.50	122.31	137.55	133.01	128.53	109.57	113.28	113.00	113.00	114.10	99.00	103.00	99.00	56.00	135.00	151.30	138.33	115.00

CHARACTER	OTU																				
	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
NOHEADS	20	9	6	17	35	26	11	9	17	23	18	12	17	8	17	10	8	20	8	27
PHYLWI	2.67	9.80	2.30	2.06	1.75	2.75	1.75	2.06	1.83	2.50	2.75	2.83	1.80	1.80	1.30	1.94	2.50	1.67	2.33	2.42
PHYLLEN	7.30	6.06	8.17	8.60	7.50	7.42	7.25	7.67	7.50	8.33	6.33	7.50	7.30	7.30	6.90	8.50	8.67	9.06	8.83	7.00
PHYLMAR	2.0	2.5	2.0	2.0	2.0	2.5	2.0	2.0	2.0	2.5	2.0	2.5	2.5	2.0	2.5	2.0	2.0	2.5	2.5	2.0
NORF	11	10	6	13	27	8	13	8	13	15	14	16	8	10	17	14	5	15	11	4
POSRF	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
RL	4.58	2.06	5.83	5.92	4.92	6.67	4.83	3.56	6.67	5.83	6.25	1.08	5.25	4.20	5.00	5.75	5.42	6.25	5.25	5.50
RW	1.92	0.80	2.17	1.33	1.08	2.17	2.33	2.50	2.08	1.75	1.30	4.40	2.12	2.20	1.00	0.92	1.08	1.67	1.67	1.67
STYLEN	7.08	4.17	6.75	6.83	7.67	8.33	7.08	5.30	6.25	6.80	5.58	4.25	5.20	7.70	4.60	7.17	8.67	5.83	5.83	7.00
LENSTBR	0.28	0.20	0.24	0.14	0.20	0.24	0.40	0.20	0.01	0.48	0.18	0.01	0.16	0.14	0.20	0.22	0.40	0.24	0.24	0.12
STYTEX	1.0	1.0	1.0	2.0	1.0	1.0	1.0	1.0	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	4.58	2.06	4.17	3.83	2.92	5.17	4.17	3.33	5.56	4.12	3.30	1.75	4.20	3.60	2.50	6.25	4.58	2.50	4.75	3.75
NODF	31	21	16	34	40	35	27	27	32	53	36	38	41	28	44	35	22	41	31	34
POSDF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	2.0	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
CORLEN	4.25	2.80	4.00	4.67	4.17	3.92	3.67	4.17	3.83	3.83	3.50	3.91	4.20	3.00	3.20	4.25	4.17	4.00	4.17	4.58
CORLBWI	0.76	0.40	0.48	0.64	1.00	0.75	0.48	0.64	0.40	0.44	0.64	0.98	0.48	0.28	0.64	0.75	0.83	0.48	0.60	0.56
STYLENG	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
LENGSTBR	10.80	6.25	7.50	8.67	11.00	10.50	10.50	5.56	9.17	9.50	9.00	7.90	7.50	7.96	7.50	13.67	9.67	8.67	9.33	10.50
STYLTEX	1.20	0.66	0.66	0.80	0.80	1.16	0.96	1.20	0.70	1.40	1.20	0.80	0.80	2.30	0.70	1.50	0.76	0.50	1.26	0.80
LENANTH	2.0	1.5	2.0	2.0	1.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPANAPP	2.64	1.20	1.76	2.48	2.33	1.92	2.04	1.80	3.83	1.92	2.00	2.28	2.40	2.00	1.70	2.32	2.00	2.08	2.20	2.42
SHPCORLB	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
PAPLENDF	4.58	4.17	6.33	4.17	4.17	3.92	5.33	2.56	3.08	4.17	2.92	2.50	3.80	3.75	3.30	6.00	4.25	3.33	3.33	5.83
DCLL	1.76	1.32	1.20	2.25	1.92	1.42	1.76	1.60	1.80	1.52	1.16	1.30	1.60	1.60	1.80	1.74	1.75	1.80	2.24	2.12
LAT	51.00	99.00	48.00	50.32	51.00	53.40	99.00	68.52	99.00	48.00	48.00	99.00	51.37	64.00	53.00	54.48	62.00	49.53	58.00	63.48
LONG	110.00	99.00	99.00	99.57	100.00	113.20	99.00	134.27	99.00	118.00	118.00	99.00	123.25	139.00	113.00	115.00	145.00	97.00	94.00	135.47

	141	142	143	145	146	147	148	149	150
NOHEADS	15	13	17	18	13	19	35	12	23
PHYLWI	2.67	2.58	1.42	1.67	3.33	1.67	2.92	2.08	2.17
PHYLLEN	8.67	9.67	8.33	8.67	9.83	8.17	7.08	7.92	7.75
PHYLMAR	2.0	2.5	2.5	2.5	2.5	2.5	2.5	2.0	2.5
NORF	13	12	12	6	13	19	18	13	10
POSRF	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
RL	7.50	7.50	6.00	4.00	6.58	3.75	4.83	5.67	7.67
RW	2.00	1.75	1.60	1.25	1.58	1.00	1.92	2.00	1.83
STYLEN	7.50	6.83	7.83	6.83	7.67	4.75	6.41	7.33	6.25
LENSTBR	0.20	0.20	0.20	0.20	0.30	0.24	0.30	0.20	0.16
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	3.75	3.33	5.08	2.08	3.75	2.00	3.75	4.33	2.92
NODF	53	32	41	35	32	35	56	43	47
POSDF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
CORLEN	3.83	4.17	4.33	3.33	3.67	0.36	3.58	3.42	4.08
CORLBWI	0.56	0.72	0.80	0.75	0.72	0.40	0.83	0.72	0.68
STYLENG	2	2	2	2	2	2	2	2	2
LENGSTBR	12.33	9.67	10.80	10.00	10.67	10.00	8.67	10.17	10.83
STYLTEX	1.00	1.20	0.76	1.10	0.92	1.08	1.40	1.26	0.80
LENANTH	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPANAPP	2.60	1.92	2.00	1.40	2.08	2.20	2.00	2.24	2.40
SHPCORLB	2	2	2	2	2	2	2	2	2
PAPLENDF	4.67	4.58	3.17	3.33	3.58	3.67	3.75	2.50	2.92
DCLL	1.60	1.88	1.48	1.58	1.16	1.20	1.67	1.58	1.82
LAT	45.40	41.00	58.50	53.00	99.00	55.04	53.25	53.00	53.00
LONG	111.00	105.00	125.11	110.00	99.00	117.17	113.08	113.00	112.00

APPENDIX THREE: DATA MATRIX FOR MORPHOMETRIC ANALYSES OF PISTILLATE CHARACTERS

MISSING DATA IS REPRESENTED BY 99, 99.0, OR 99.00.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
NOHEADS	10	8	10	8	10	9	13	10	11	10	11	8	8	6	8	8	18	17	12	10
PHYLWI	1.67	2.56	2.82	1.83	2.56	2.42	2.75	2.50	1.67	1.33	2.00	2.56	2.00	2.33	1.67	2.50	3.25	1.76	1.67	2.00
PHYLLEN	5.42	6.06	5.63	6.00	6.67	6.75	6.33	7.67	5.00	6.67	5.41	6.67	5.90	7.56	5.63	6.33	7.06	4.56	6.42	5.63
PHYLLMAR	2.00	2.00	2.00	2.50	2.50	2.50	2.00	2.00	2.50	2.00	2.50	2.50	2.50	2.00	2.00	2.50	2.00	2.50	2.00	2.00
NORF	78	60	67	105	71	74	102	76	43	75	69	63	60	64	66	69	63	46	63	69
POSRF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
RL	0.96	2.40	2.00	2.92	3.92	1.60	3.00	1.28	1.04	1.20	1.40	2.50	1.52	1.60	1.12	1.60	1.40	2.80	0.80	1.60
RW	0.24	0.60	0.44	0.40	1.17	0.30	0.56	0.20	0.24	0.24	0.36	0.67	0.40	0.40	1.00	0.36	0.28	0.40	0.10	0.30
STYLEN	7.20	4.92	7.06	9.00	8.33	8.33	10.00	7.06	5.67	5.75	5.42	7.50	5.50	7.17	6.50	6.50	7.50	5.83	5.00	6.50
LENSTBR	0.16	0.24	0.24	0.30	0.16	0.20	0.54	0.24	0.24	0.16	0.14	0.20	0.28	0.24	0.32	0.20	0.40	0.20	0.24	0.20
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	4.17	2.33	5.42	7.50	3.83	5.00	15.00	3.67	4.16	4.56	3.50	6.25	3.50	3.33	3.92	4.50	8.33	3.30	6.25	3.56
ACHLEN	1.33	1.17	1.17	1.25	0.92	1.56	2.67	1.33	0.96	1.67	1.67	1.60	1.10	1.08	2.42	1.00	2.17	0.63	2.08	1.08
NODF	1	2	3	3	2	1	5	3	2	3	2	2	2	3	3	6	3	2	5	3
POSDF	2.1	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
CORLEN	2.25	2.92	3.83	2.75	3.20	2.75	3.67	3.16	2.60	2.08	2.33	3.75	1.60	3.20	2.32	2.64	2.40	1.24	2.00	2.68
CORLBWI	0.32	0.40	0.64	0.48	0.60	0.60	0.40	0.52	0.56	0.32	0.44	0.60	0.36	0.80	0.80	0.30	0.40	0.44	0.20	0.70
STYLENG	5.83	5.83	7.25	6.92	6.25	7.00	6.58	6.58	3.83	5.30	4.83	6.92	4.83	6.83	4.83	6.41	7.42	5.50	5.50	6.42
LENGSTBR	0.80	0.56	0.60	0.60	0.80	0.70	1.24	0.80	0.26	0.18	0.40	1.04	0.38	0.68	0.00	0.70	0.70	0.68	0.80	0.70
STYLTEX	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	1.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	1.5	2.0
LENANTH	0.70	0.88	1.28	0.79	0.84	0.92	1.40	0.88	0.50	1.00	0.48	0.88	0.80	1.00	0.70	1.00	1.28	1.08	0.78	0.84
SHPANAPP	2.0	2.0	2.0	3.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPCORLB	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
PAPLENDF	3.30	2.92	6.00	5.00	3.33	3.75	6.67	3.33	3.40	3.83	2.08	5.17	2.83	2.83	3.75	2.50	6.25	3.17	3.92	4.17
DCLL	1.00	1.08	1.44	1.20	1.44	0.88	1.56	1.44	0.72	1.20	4.40	1.52	0.60	1.28	0.80	1.20	1.40	1.32	0.52	1.24
LAT		61.13	54.45	60.23	63.54	63.34	64.50	63.31	59.56	99.00	70.16	68.15	60.00	63.34	71.00	62.11	68.06	62.22	68.22	99.00
LONG	147.52	149.53	165.00	166.11	142.15	142.20	147.51	149.55	141.42	99.00	161.55	166.00	166.00	148.41	156.00	131.47	136.28	145.15	133.44	99.00

CHARACTER	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
NOHEADS	5	6	7	6	9	8	10	8	9	9	11	14	10	6	19	10	11	9	9	14
PHYLWI	2.50	2.67	1.83	1.67	1.20	2.17	2.50	1.83	1.84	2.50	2.08	2.42	1.67	2.25	1.25	1.68	2.33	1.92	3.33	2.08
PHYLLEN	5.00	5.50	5.17	5.17	6.17	6.42	6.50	6.00	5.91	7.75	6.67	6.92	5.25	7.00	6.25	5.17	7.92	5.00	6.33	7.08
PHYLLMAR	2.00	2.00	2.50	2.50	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.50	2.50	2.00	2.00	2.00	2.50
NORF	60	66	55	75	97	61	85	46	91	52	81	81	57	65	90	77	78	109	101	57
POSRF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.0	1.5	1.5	1.5	1.5	1.5	1.5	1.5
RL	1.60	4.83	1.12	1.67	1.50	1.32	1.68	1.04	1.83	1.15	2.00	1.28	2.20	1.40	1.24	1.52	3.17	1.44	1.76	3.67
RW	0.48	0.30	0.28	0.48	0.42	0.32	0.32	0.22	0.33	0.27	0.56	0.32	0.32	0.32	0.36	0.50	0.80	0.36	0.60	0.50
STYLEN	4.75	6.25	4.83	7.08	7.67	5.83	6.42	5.83	6.08	5.90	5.42	6.00	7.08	6.92	6.67	7.17	7.92	4.58	6.83	6.80
LENSTBR	0.20	0.20	0.26	0.24	0.16	0.14	0.36	0.16	0.24	0.20	0.36	0.24	0.48	0.30	0.16	0.24	0.36	0.14	0.30	0.20
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	3.33	4.17	2.50	4.17	7.83	4.17	5.92	4.17	3.83	5.21	3.33	6.25	6.00	6.67	3.30	5.25	3.50	2.17	5.42	2.08
ACHLEN	0.80	1.00	1.17	1.33	1.00	1.42	1.33	1.00	1.75	1.33	1.25	1.67	0.92	1.33	1.00	1.50	1.58	1.25	1.50	1.33
NODF	2	2	1	1	4	3	3	5	3	5	2	3	2	5	2	4	5	3	12	3
POSDF	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.1	2.0	2.0	2.0	2.0	2.0
CORLEN	2.60	2.62	1.16	2.63	2.17	2.62	2.60	3.20	3.17	3.00	2.12	2.56	1.60	2.88	3.58	2.90	3.20	2.32	3.56	3.17
CORLBWI	0.36	0.60	0.56	0.52	0.20	0.53	0.40	0.44	0.40	0.40	0.30	0.60	0.24	0.40	0.40	0.40	0.44	0.36	0.24	0.75
STYLENG	4.58	5.58	3.25	6.00	6.42	5.50	5.83	6.17	6.08	7.50	6.42	6.67	2.60	5.67	6.08	5.80	6.25	5.67	7.08	5.42
LENGSTBR	0.30	0.70	0.50	0.46	0.40	0.28	0.60	0.60	0.50	0.70	0.80	0.70	0.46	0.90	0.60	0.30	0.70	0.50	0.50	0.28
STYLTEX	2.0	2.0	2.0	2.0	1.0	1.5	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
LENANTH	0.80	0.96	0.72	1.00	0.72	0.60	0.80	0.92	0.80	1.16	1.00	0.96	0.90	0.84	0.92	1.00	0.82	0.70	1.40	1.16
SHPANAPP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	2.0	3.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPCORLB	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
PAPLENDF	3.92	3.33	2.25	3.75	0.50	3.33	4.75	5.00	3.75	5.83	2.92	4.17	1.56	4.17	3.40	3.75	3.83	2.40	4.58	2.83
DCLL	1.20	1.04	1.28	3.00	0.72	0.90	1.04	0.92	1.40	1.40	1.12	1.08	0.70	1.70	1.00	1.20	1.32	0.88	0.98	2.08
LAT	71.00	63.00	60.25	65.48	63.58	57.13	69.50	67.55	56.00	64.23	64.08	99.00	67.22	71.16	61.00	58.18	59.38	64.29	65.29	59.33
LONG	56.00	150.00	172.36	168.00	135.42	133.27	155.30	98.40	169.00	138.21	141.20	99.00	102.10	156.50	149.00	152.24	151.33	146.45	145.25	139.44

CHARACTER	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
NOHEADS	16	11	8	9	7	14	8	9	8	8	10	13	6	12	10	12	13	13	16	9
PHYLWI	1.92	1.50	1.67	1.75	2.67	1.70	1.80	1.80	2.00	2.00	1.58	1.58	1.83	2.50	1.33	2.42	1.75	1.92	1.17	2.17
PHYLLEN	5.33	7.00	6.25	6.06	7.08	6.00	7.70	6.30	4.80	6.25	6.42	7.50	7.92	6.67	5.58	5.00	6.00	6.75	6.67	6.67
PHYLLMAR	2.50	2.50	2.00	2.00	2.00	2.00	2.00	2.50	2.00	2.00	2.00	2.00	2.00	2.50	2.00	2.00	2.00	2.00	2.00	2.50
NORF	65	64	46	63	92	67	64	79	87	80	48	96	85	77	63	56	60	30	75	64
POSRF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
RL	1.20	1.00	2.83	1.40	2.00	1.67	2.00	1.60	3.30	0.94	2.40	2.06	1.60	2.08	2.08	1.88	0.94	4.06	2.00	2.68
RW	0.20	0.16	0.52	0.36	0.50	0.72	0.24	0.20	0.72	0.24	0.36	0.34	0.40	0.40	0.44	0.32	0.20	0.88	0.20	0.48
STYLEN	6.58	7.50	6.75	6.50	7.67	7.50	7.25	6.70	4.60	5.58	6.67	7.33	6.60	8.00	8.00	6.67	6.83	8.33	7.00	6.67
LENSTBR	0.28	0.30	0.20	0.20	0.60	0.26	0.30	0.30	0.14	0.22	0.20	0.26	0.32	0.40	0.22	0.28	0.22	0.20	0.40	0.16
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	4.42	6.50	2.50	4.33	4.58	6.00	3.80	3.58	1.90	5.42	3.25	6.42	4.17	7.50	2.75	2.66	3.50	5.17	3.56	5.00
ACHLEN	1.06	1.25	1.06	1.25	1.25	1.00	1.00	0.12	0.84	2.00	1.32	1.20	1.67	1.67	1.58	1.00	1.75	1.67	0.80	1.25
NODF	2	2	3	2	1	2	2	2	4	3	3	3	2	2	2	6	3	2	3	4
POSDF	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
CORLEN	2.60	2.50	1.92	2.50	3.08	2.30	1.00	3.90	3.10	2.50	2.40	3.33	2.60	2.75	2.24	2.67	2.52	2.75	2.48	3.04
CORLBWI	0.60	0.32	0.60	0.60	0.60	0.36	0.32	0.36	0.40	0.34	0.60	0.42	0.40	0.28	0.56	0.68	0.48	0.48	0.40	0.56
STYLENG	5.42	7.12	5.67	6.50	7.08	5.90	6.60	5.00	5.00	6.00	5.25	6.33	6.25	5.83	5.83	4.83	4.83	6.42	6.67	5.58
LENGSTBR	0.50	0.55	0.00	0.34	0.60	0.34	0.40	0.84	0.60	0.40	0.50	1.00	0.60	1.00	0.54	0.30	0.40	0.44	0.44	0.38
STYLTEX	2.0	2.0	1.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
LENANTH	0.72	0.88	0.92	0.80	0.92	0.70	1.04	1.28	0.84	1.06	1.00	1.00	0.84	0.84	1.00	1.52	1.12	0.92	1.12	1.08
SHPANAPP	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPCORLB	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0
PAPLENDF	4.83	4.17	3.17	2.56	4.17	3.70	1.50	2.50	2.70	3.67	3.28	4.17	3.92	4.58	3.20	2.50	2.06	3.75	3.75	2.92
DCLL	1.08	1.40	1.20	0.36	1.36	0.92	0.56	1.40	1.40	0.86	0.36	1.40	1.24	0.96	1.00	1.42	1.12	0.80	1.12	1.68
LAT	61.00	65.23	90.00	90.00	60.26	49.00	56.00	51.20	58.00	50.00	58.00	61.37	56.54	62.06	53.25	53.25	54.35	51.00	57.20	59.00
LONG	159.55	167.09	90.00	90.00	149.17	122.00	129.00	116.13	129.00	122.00	129.00	133.03	123.48	137.17	90.00	90.00	121.05	115.00	153.22	129.00

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
NOHEADS	10	8	6	10	6	6	8	12	9	6	11	8	18	10	42	31	15	21	22	17
PHYLWI	1.50	1.67	1.75	2.33	2.33	2.42	1.67	1.33	1.56	1.67	2.08	1.72	0.83	2.17	1.67	2.25	1.25	2.08	1.92	1.67
PHYLLEN	6.75	5.08	6.75	6.75	7.08	8.33	6.00	6.42	6.17	5.50	6.83	1.67	5.08	8.17	7.50	9.00	6.25	7.50	8.67	4.33
PHYLLMAR	2.00	2.00	2.00	2.00	2.00	2.00	2.50	2.50	2.50	2.50	2.00	2.00	2.50	2.00	1.00	1.00	1.00	1.00	1.00	2.50
NORF	58	61	56	83	90	75	60	60	85	63	62	70	62	58	92	104	75	68	103	60
POSRF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
RL	1.82	2.26	0.96	1.44	2.00	1.60	1.52	1.36	1.36	2.67	3.00	1.44	1.40	0.50	5.42	4.08	3.20	2.92	4.00	0.34
RW	0.24	0.52	0.20	0.34	0.28	0.32	0.20	0.14	0.40	0.40	0.36	0.48	0.18	0.20	0.42	0.64	0.56	0.52	0.76	0.16
STYLEN	5.58	7.08	6.17	6.33	6.17	7.33	7.00	7.42	6.83	6.92	6.33	6.33	6.67	8.50	7.17	7.16	7.50	6.25	7.75	5.58
LENSTBR	0.08	0.14	0.20	0.20	0.30	0.36	0.24	0.16	0.36	0.48	0.20	0.20	0.20	0.36	0.08	0.20	0.16	0.08	0.14	0.22
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	6.25	4.17	10.33	4.92	3.33	5.42	9.17	6.08	3.75	3.33	4.67	7.25	8.33	3.30	5.83	5.17	2.92	3.54	4.33	5.00
ACHLEN	2.08	1.33	2.32	1.83	1.50	1.25	1.83	1.25	1.25	1.58	1.50	1.50	1.83	1.75	1.40	1.67	1.50	1.67	1.33	1.25
NODF	2	2	5	6	4	3	5	3	2	2	2	3	2	3	2	3	2	2	1	2
POSDF	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
CORLEN	0.26	2.44	2.40	2.48	2.96	2.80	1.80	2.68	5.75	2.33	2.50	6.83	3.00	2.00	3.75	3.40	3.75	3.28	3.72	2.20
CORLBWI	0.30	0.36	0.46	0.32	0.33	0.40	0.40	0.40	0.36	0.32	0.30	0.80	0.46	0.22	0.56	0.52	0.60	0.46	0.64	0.40
STYLENG	5.00	4.92	5.83	5.42	6.33	5.00	7.16	7.08	7.33	5.48	7.08	7.33	4.83	5.00	7.08	8.30	6.67	5.08	7.83	5.67
LENGSTBR	0.42	0.48	0.40	0.30	0.76	0.54	0.40	0.70	0.40	0.70	0.76	0.52	0.80	0.38	0.10	0.10	0.00	0.40	0.00	0.46
STYLTEX	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.5	1.0	1.0	1.0	1.5	1.0	2.0
LENANTH	1.20	1.24	0.88	1.04	1.20	0.40	0.52	0.60	0.80	1.24	1.40	1.00	1.40	1.00	0.90	0.96	1.20	1.00	0.88	0.80
SHPANAPP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPCORLB	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
PAPLENDF	3.83	4.22	6.33	3.00	3.06	4.00	7.50	3.06	3.33	3.75	3.92	5.50	6.08	2.28	5.42	4.42	3.30	2.75	3.10	4.50
DCLL	1.22	0.72	1.46	0.86	0.96	1.02	1.40	1.28	1.10	1.52	1.04	1.40	1.20	0.52	2.40	2.40	2.25	1.72	2.40	1.90
LAT	51.00	51.00	50.00	90.00	90.00	70.03	65.56	63.25	63.41	52.40	53.00	60.59	56.00	57.05	90.00	43.00	47.00	45.30	47.00	57.00
LONG	115.00	116.00	122.00	90.00	90.00	157.15	137.24	142.30	144.16	116.15	112.00	136.23	111.00	122.35	90.00	124.00	124.00	122.29	119.00	126.05

CHARACTER	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
NOHEADS	20	22	15	16	21	14	27	6	20	25	39	16	21	10	20	12	13	11	17	22
PHYLWI	1.50	1.83	1.67	0.67	1.25	1.67	1.17	2.67	2.00	1.67	2.33	1.20	1.33	2.42	1.67	1.83	2.17	1.75	1.67	2.25
PHYLLEN	1.00	6.90	3.75	1.00	6.42	5.08	5.67	6.67	6.00	4.17	7.08	3.83	6.25	7.50	4.00	4.67	9.50	9.50	6.08	5.50
PHYLLMAR	1.00	1.00	1.00	1.00	2.00	2.00	2.50	2.00	2.50	2.00	1.00	2.00	1.00	2.50	2.00	2.50	1.00	2.50	2.00	2.50
NORF	65	89	60	105	72	78	54	101	59	94	103	125	90	100	76	51	70	70	70	100
POSRF	1.5	1.5	1.0	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
RL	1.72	1.40	1.20	1.90	0.68	1.17	1.16	0.76	1.92	1.12	6.33	1.52	4.25	0.00	0.20	0.32	0.00	0.00	1.28	1.44
RW	0.32	0.26	0.32	0.25	0.16	0.24	0.40	0.20	0.34	0.32	0.83	0.36	0.68	0.00	0.20	0.20	0.00	0.00	0.28	0.48
STYLEN	6.33	6.90	2.40	1.60	7.92	5.25	4.42	6.33	7.67	5.17	7.92	4.00	5.00	9.60	6.41	7.42	8.33	9.17	5.58	5.67
LENSTBR	0.20	0.58	0.06	0.06	0.20	0.16	0.16	0.80	0.26	0.20	0.40	0.20	0.20	0.42	0.20	0.10	0.28	0.14	0.14	0.22
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	6.25	8.67	3.75	2.70	5.83	3.17	3.33	4.42	6.41	4.17	3.17	3.75	2.00	6.08	9.17	11.80	10.00	3.75	2.17	5.00
ACHLEN	1.33	1.33	0.60	0.75	1.33	1.17	0.92	1.08	1.08	1.00	1.17	1.12	1.20	2.50	1.00	1.67	3.50	1.67	0.68	0.83
NODF	1	1	1	3	1	5	2	2	1	1	5	1	3	2	2	2	1	2	2	2
POSDF	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
CORLEN	2.40	2.44	3.20	2.30	2.75	2.84	2.33	3.12	2.67	3.08	2.50	2.36	3.28	2.64	2.60	2.00	2.64	2.60	2.88	2.40
CORLBWI	0.52	0.62	0.20	0.28	0.42	0.60	0.60	0.52	0.36	0.40	0.56	0.56	0.44	0.56	0.36	0.40	0.40	0.30	0.44	0.52
STYLENG	6.33	4.75	1.90	6.70	7.67	3.75	5.58	5.33	7.50	4.48	6.67	3.60	5.00	7.67	5.30	4.17	6.83	6.67	5.42	6.67
LENGSTBR	0.14	0.00	0.40	0.02	0.40	0.26	0.34	0.40	0.52	0.48	0.36	0.36	0.44	0.36	0.52	0.36	0.34	0.18	0.30	0.40
STYLTEX	1.5	1.5	2.0	1.0	2.0	2.0	2.0	2.0	2.0	1.5	2.0	2.0	2.0	2.0	2.0	1.0	1.5	1.5	2.0	1.0
LENANTH	0.70	0.80	1.40	0.90	1.08	1.40	1.48	1.52	1.40	1.00	1.40	0.96	1.08	0.80	1.12	1.00	1.02	1.04	1.30	0.88
SHPANAPP	2.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0
SHPCORLB	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
PAPLENDF	5.42	6.91	4.00	3.20	6.25	2.50	4.58	4.67	5.53	4.58	2.92	3.33	1.67	3.50	6.17	5.60	2.20	2.50	2.50	5.17
DCLL	1.40	1.00	1.47	1.67	1.48	1.84	1.67	2.48	2.04	1.04	1.28	1.40	2.88	1.28	1.60	1.32	1.80	1.50	1.68	1.64
LAT	48.00	53.16	53.46	49.00	47.00	99.00	49.00	53.00	51.00	42.00	37.21	53.00	37.00	99.00	55.00	57.03	65.46	66.33	61.00	60.03
LONG	123.00	60.25	113.10	123.00	89.00	99.00	83.00	115.00	115.00	73.00	121.58	80.00	121.00	99.00	120.00	122.31	137.55	136.20	133.01	128.53

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
NOHEADS	16	30	11	25	22	26	34	23	19	13	16	19	9	21	34	22	23	17	14	21
PHYLWI	2.50	0.83	1.83	1.92	1.67	1.83	2.70	1.40	1.25	2.50	1.40	2.08	1.08	1.83	1.92	1.17	2.17	2.08	1.40	1.75
PHYLLEN	5.75	4.42	9.00	6.83	7.50	6.67	6.83	6.70	5.58	6.83	5.42	5.50	3.92	4.33	5.42	5.00	8.50	5.17	6.08	6.67
PHYLLMAR	2.50	2.50	2.50	2.50	1.00	2.00	2.00	2.00	2.00	2.50	2.50	2.50	2.00	2.50	2.50	2.00	2.50	2.00	2.50	2.00
NORF	95	72	59	63	52	79	73	65	75	68	70	62	46	80	69	57	73	69	90	124
POSRF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.0	1.5	1.5	1.5	1.5	1.5	1.5
RL	2.83	1.00	2.00	2.80	1.68	1.80	2.50	2.50	1.52	1.20	1.20	1.84	0.80	2.00	2.00	1.80	2.64	2.60	1.56	2.80
RW	0.76	0.18	0.26	0.67	0.32	0.38	0.64	0.48	0.18	0.20	0.32	0.68	0.24	0.40	0.56	0.36	0.80	0.40	0.30	0.68
STYLEN	6.58	5.42	7.06	7.17	6.42	5.83	6.67	5.50	5.67	7.50	5.08	6.25	5.42	5.08	5.25	6.25	9.83	6.67	5.00	5.50
LENSTBR	0.26	0.24	0.20	0.24	0.24	0.14	0.28	0.10	0.14	0.30	0.30	0.14	0.28	0.22	0.16	0.26	0.30	0.30	0.10	0.22
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	5.42	3.83	7.67	6.67	4.12	4.17	5.00	4.25	6.90	3.33	2.20	6.96	2.52	3.60	4.42	3.67	7.50	5.00	3.40	2.75
ACHLEN	1.25	0.66	1.42	1.25	1.42	1.25	0.92	1.70	1.50	1.08	0.60	1.25	1.42	0.92	0.83	1.64	1.60	1.08	0.56	1.08
NODF	5	1	4	2	3	2	1	2	3	3	4	2	1	2	1	3	1	3	3	5
POSDF	2.0	2.0	2.0	2.0	2.0	2.1	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.1	2.0	2.0	2.0
CORLEN	2.92	2.40	3.00	3.17	2.83	2.75	3.03	2.48	2.40	2.80	2.32	2.20	2.60	2.32	2.80	2.40	2.40	2.80	1.60	2.90
CORLBWI	0.56	0.40	0.36	0.60	0.44	0.52	0.52	0.28	0.44	0.56	0.40	0.24	0.44	0.72	0.40	0.52	0.38	0.24	0.28	0.40
STYLENG	6.58	5.50	6.42	6.67	7.25	6.83	6.67	5.83	5.00	6.92	4.33	5.67	5.50	4.00	5.00	6.75	6.67	5.42	3.36	9.20
LENGSTBR	0.80	0.60	0.40	0.46	0.40	0.50	0.68	0.34	0.36	1.20	0.50	0.40	0.40	0.50	0.60	0.60	0.70	0.44	0.70	0.68
STYLTEX	2.0	2.0	2.0	2.0	1.0	2.0	2.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
LENANTH	1.40	1.28	1.40	1.36	0.88	1.20	1.08	0.80	1.04	1.00	1.12	0.94	0.88	1.20	1.28	1.20	0.86	0.80	0.92	0.76
SHPANAPP	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
SHPCORLB	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
PAPLENDF	4.17	3.75	5.83	5.83	3.50	5.17	5.00	5.20	5.67	4.17	2.02	5.17	2.25	2.80	4.33	4.17	5.83	5.33	1.80	3.58
DCLL	1.80	1.60	1.84	2.12	1.92	1.80	2.04	1.52	1.28	1.32	0.80	1.00	1.08	1.20	1.08	1.60	1.10	1.00	0.40	1.67
LAT	57.49	55.35	99.00	54.46	99.00	99.00	47.00	47.00	53.00	99.00	55.16	51.00	61.00	51.00	54.08	53.40	99.00	66.44	57.05	99.00
LONG	109.57	128.50	99.00	111.56	99.00	99.00	122.00	122.00	113.00	99.00	85.12	115.00	132.00	100.00	125.21	113.20	99.00	143.34	122.35	99.00

CHARACTER	121	122	123	124	125	126	127	128	129	130	131	132
NOHEADS	14	25	11	13	13	24	26	27	23	34	22	6
PHYLWI	1.67	2.33	1.42	1.92	1.08	1.00	1.58	1.67	3.08	1.83	1.75	1.08
PHYLLEN	6.58	8.00	3.75	7.08	7.75	6.17	6.33	5.08	7.33	6.00	4.42	5.00
PHYLLMAR	2.00	2.00	2.00	2.50	2.50	2.50	2.00	2.50	2.50	2.00	2.50	2.00
NORF	69	96	76	61	31	75	114	68	94	66	139	54
POSRF	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
RL	2.58	2.48	0.80	1.92	0.58	2.04	2.32	2.67	5.42	2.12	2.00	2.20
RW	0.32	0.52	0.36	0.40	0.14	0.32	0.28	0.83	0.75	0.24	0.68	0.52
STYLEN	7.83	3.92	4.17	6.25	7.92	7.08	6.92	5.83	5.17	7.27	5.41	5.00
LENSTBR	0.36	0.16	0.16	0.24	0.20	0.20	0.42	0.20	0.30	0.30	0.14	0.18
STYTEX	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PAPLENRF	5.00	3.83	14.00	4.33	17.33	6.67	6.67	3.50	4.83	2.50	1.92	1.67
ACHLEN	1.20	0.83	1.00	0.92	2.75	1.33	1.25	0.83	1.17	1.00	1.50	1.25
NODF	4	4	3	2	2	3	2	2	5	3	4	2
POSDF	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
CORLEN	3.75	2.00	2.32	2.28	3.28	2.48	2.00	2.75	2.50	3.17	2.16	2.33
CORLBWI	0.38	0.40	0.60	0.48	0.48	0.26	0.40	0.40	0.60	0.60	0.44	0.44
STYLENG	7.25	4.00	4.58	6.25	7.92	6.25	5.25	1.17	5.33	7.50	4.17	4.50
LENGSTBR	0.64	0.60	0.26	0.60	0.50	0.46	0.64	0.60	0.70	1.32	0.50	0.60
STYLTEX	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
LENANTH	1.20	0.80	1.02	0.82	1.90	0.92	1.25	1.00	0.80	1.00	0.84	0.68
SHPANAPP	2.0	2.0	3.0	2.0	2.0	2.0	2.0	2.0	2.0	3.0	2.0	2.0
SHPCORLB	2.0	2.0	1.5	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
PAPLENDF	4.17	3.33	1.83	2.75	11.33	5.00	5.08	2.50	4.17	3.75	2.75	2.16
DCLL	1.84	0.60	0.96	1.20	1.32	1.08	1.40	0.60	1.16	1.75	1.20	0.60
LAT	99.00	56.00	45.00	62.39	58.50	62.04	63.20	53.25	60.00	49.34	53.25	99.00
LONG	99.00	94.00	93.11	160.12	125.11	132.19	142.52	113.30	111.53	110.08	113.08	99.00

NOHEADS
PHYLWI
PHYLLEN
PHYLLMAR
NORF
POSRF
RL
RW
STYLEN
LENSTBR
STYTEX
PAPLENRF
ACHLEN
NODF
POSDF
CORLEN
CORLBWI
STYLENG
LENGSTBR
STYLTEX
LENANTH
SHPANAPP
SHPCORLB
PAPLENDF
DCLL
LAT
LONG

APPENDIX FOUR: CORRELATION MATRIX FOR DISCRIMINANT ANALYSIS OF LEAF CHARACTERS

CHARACTER	SHAPE	MAXW	MAXL	APWID	APANGL	BAPANGL	NO1LOB	NO2LOB	LBAPSHP
SHAPE	1.00000								
MAXW	-.10062	1.00000							
MAXL	-.17476	.92320	1.00000						
APWID	.05100	.56134	.55321	1.00000					
APANGL	.07088	.21649	.12472	.09550	1.00000				
BAPANGL	.09357	.01953	.05868	-.06965	-.06827	1.00000			
NO1LOB	-.17783	.13019	.13280	.06783	.11263	-.15263	1.00000		
NO2LOB	-.08546	.19091	.19296	.13471	.15632	-.15944	.35695	1.00000	
LBAPSHP	.16473	-.06008	-.06084	-.03425	.05143	.06740	-.20584	-.07239	1.00000
NOTETH	-.09175	.42270	.40196	.06261	.19710	-.06356	.03020	.14041	.02096
TETHSHP	.00364	-.08439	-.06698	-.05005	.06206	.06163	-.04664	-.08865	-.00910
SINDEP	-.09836	.63023	.56285	.34278	.05960	-.03052	.16868	.26409	-.05529
SINWID	.02036	.21702	.20176	.11647	.13304	.04814	.17278	-.01497	-.07391
SINSHP	.01732	-.10912	-.12113	-.08690	.05268	.07236	.30243	-.03131	-.16895
PERI	-.07983	.88606	.83143	.49428	.14756	-.03352	.16382	.24989	-.04695
PUBAD	-.04424	-.04588	-.03854	-.03172	-.05890	-.03372	.01656	-.00963	-.01578
PUBAB	.02812	.04795	.04699	.01189	.02978	.02407	-.15417	-.02145	-.03927

CHARACTER	NOTETH	TETHSHP	SINDEP	SINWID	SINSHP	PERI	PUBAD	PUBAB
SHAPE								
MAXW								
MAXL								
APWID								
APANGL								
BAPANGL								
NO1LOB								
NO2LOB								
LBAPSHP								
NOTETH	1.00000							
TETHSHP	-.17809	1.00000						
SINDEP	.29601	-.07499	1.00000					
SINWID	-.06511	.01550	.16231	1.00000				
SINSHP	-.07586	.03633	-.08507	.18426	1.00000			
PERI	.43734	-.12315	.70911	.16902	-.12747	1.00000		
PUBAD	-.02041	-.00997	-.00022	-.04356	-.00334	-.03503	1.00000	
PUBAB	.05719	-.04575	-.00947	-.05701	-.04564	.06550	-.14212	1.00000

APPENDIX FIVE: CORRELATION MATRIX FOR DISCRIMINANT ANALYSIS OF STAMINATE CHARACTERS

CHARACTER	NOHEADS	PHYLW	PHYLL	PHYLWAR	NORF	POSRF	RL	RW	STYLEN	LENSTBR	STYTEX	PAPLENRF
NOHEADS	1.00000											
PHYLW	-.06246	1.00000										
PHYLL	-.02634	.10586	1.00000									
PHYLWAR	-.07983	-.03186	-.23159	1.00000								
NORF	.17681	.07197	-.13320	.09051	1.00000							
POSRF	-.03140	.08833	.10098	.03479	.14749	1.00000						
RL	-.04922	-.09747	.26377	.10006	-.05580	-.17536	1.00000					
RW	-.14203	.01328	.01813	.05432	-.08775	.01239	.23332	1.00000				
STYLEN	.01439	-.07061	.31622	-.02906	-.04389	.00019	.41141	.09324	1.00000			
LENSTBR	.03062	-.09367	.11424	-.00794	-.08351	.07769	-.02227	-.14027	.13373	1.00000		
STYTEX	.01992	-.03947	-.02573	-.05887	.01621	-.03184	.15348	-.03472	.07213	-.11313	1.00000	
PAPLENRF	-.13471	-.06441	.22262	.01525	-.10790	.00075	.32461	.15043	.36041	.19863	.07687	1.00000
NODF	.32854	.08912	.19654	-.19620	-.01182	.01774	-.01311	-.08214	.01903	-.03189	.04535	-.04641
POSDF	-.04504	.04295	.13185	-.22759	.20687	.07620	-.07984	-.06756	-.12006	.07009	-.02871	-.03040
CORLEN	-.12157	-.06753	.23436	.06304	-.09209	-.03756	.40996	.20697	.38841	-.03138	.07739	.26746
CORLBW	-.06611	.04166	.11877	.04041	-.06992	.41700	-.08286	-.11111	.16996	.24153	-.00694	.09147
SHPCORLB	-.08250	-.06369	.03394	.12478	-.13108	-.00677	.01270	.05836	-.02618	.00566	.00000	.07015
STYLENG	-.01730	-.10184	.11842	-.07620	-.09794	-.00064	.35057	-.09746	.35636	.11153	.07873	.24520
LENGSTBR	-.01394	-.01757	-.16444	.34333	.00648	.01477	-.00918	.05042	.01330	.04084	-.12760	.01323
STYLTEX	-.11138	-.13508	-.23765	.56027	.17977	.05119	.06163	.07114	-.03726	.00908	-.01088	.06828
ANLEN	.10403	-.13501	.20567	.16328	-.12387	-.07843	.20892	.05857	.29458	.02266	.19568	.15116
SHPANAPP	.06787	.09745	-.06908	-.06804	-.01510	-.03383	-.05710	.07876	.00300	-.07191	-.01942	.05256
PAPLENDF	-.11623	-.03111	.25879	-.08592	-.14485	-.00738	.27803	.01418	.28030	.15322	.02174	.58413
DCLL	.11162	-.05018	.14266	-.09656	-.05780	-.01535	.12287	-.05019	.28977	.12951	.11118	.12547

CHARACTER	NODF	POSDF	CORLEN	CORLBW	SHPCORLB	STYLENG	LENGSTBR	STYLTEX	ANLEN	SHPANAPP	PAPLENDF	DCLL
NODF	1.00000											
POSDF	.02919	1.00000										
CORLEN	.04559	-.04063	1.00000									
CORLBW	.12596	-.04633	.07738	1.00000								
SHPCORLB	-.01000	-.03395	-.03677	-.03062	1.00000							
STYLENG	-.04708	.07841	.30750	.09817	-.05679	1.00000						
LENGSTBR	-.02059	-.18309	-.02988	.08658	.02561	-.09216	1.00000					
STYLTEX	-.28439	-.17022	.07905	.02899	.12105	-.09319	.35934	1.00000				
ANLEN	-.04592	-.27357	.30052	.02422	.02332	.04780	.14614	.29567	1.00000			
SHPANAPP	.14001	-.02498	-.07669	.01306	-.01444	-.05033	-.10724	-.17183	-.23146	1.00000		
PAPLENDF	.02836	-.04587	.23423	.15308	-.05705	.35387	-.12558	-.13666	.05116	.02731	1.00000	
DCLL	.04584	-.04298	.33705	.04072	-.11487	.24445	.04553	-.12809	.31995	-.01217	.22231	1.00000

APPENDIX SIX: CORRELATION MATRIX FOR DISCRIMINANT ANALYSIS OF PISTILLATE CHARACTERS

CHARACTER	NOHEADS	PHYLWI	PHYLLEN	PHYLWAR	NORF	POSRF	RL	RW	STYLEN	LENSTBR	STYTEX	PAPLENRF
NOHEADS	1.00000											
PHYLWI	.03838	1.00000										
PHYLLEN	.07158	.41366	1.00000									
PHYLWAR	-.16661	-.01739	-.06701	1.00000								
NORF	.23206	.17909	.04157	-.15543	1.00000							
POSRF	.04985	.03313	.17147	.08891	.07286	1.00000						
RL	.47399	.24168	.17948	-.32491	.19468	.00336	1.00000					
RW	.25569	.28474	.05344	-.13546	.20161	.02320	.64619	1.00000				
STYLEN	.02821	.23261	.47936	.09057	-.06166	.18253	.08848	.02194	1.00000			
LENSTBR	-.05528	.33006	.23332	.01780	.15742	-.03046	-.01297	-.03517	.35055	1.00000		
STYTEX	.00157	-.12195	.02213	-.03587	.01833	.00826	-.05741	-.06918	-.07053	-.07654	1.00000	
PAPLENRF	-.07646	.04668	.13700	.08658	-.14445	.01624	-.22935	-.20813	.40271	.13265	-.00865	1.00000
ACHLEN	-.14370	.07126	.36751	-.12078	-.05765	.16416	-.17384	-.13279	.42351	.10613	.06078	.51092
NODF	-.01025	.27158	.16985	-.08198	.19701	.08655	.10529	.12066	-.00942	.00007	-.00171	.03483
POSDF	.13986	-.05234	.07319	.02328	.05312	.03601	-.05018	.02685	.13278	-.07274	-.01437	-.00875
CORLEN	.05817	.16404	.03905	-.11078	.16262	.06719	.16143	.21117	.24060	.05955	-.07602	.05569
CORLBWI	.10974	.17021	-.03517	-.02369	-.05457	.08500	.22990	.23193	.06142	.04174	-.08968	-.09923
STYLENG	.13057	.18818	.39974	-.09474	.11147	.37502	.13470	.01470	.51024	.11961	-.04698	.19587
LENGSTBR	.08889	.32183	.15416	.25051	.12735	.02142	.02472	-.06157	.19133	.22699	-.15310	.08552
STYLTEX	-.04866	.06188	-.04443	.29624	-.03375	-.08903	-.04699	-.08721	-.00383	.14447	.03361	.00730
LENANTH	.09555	.12882	.07763	.10370	-.05333	-.09214	.10124	-.00341	.04270	.15451	.02757	.03798
SHPANAPP	-.00906	.08482	.10843	.01549	-.07886	.01415	-.08583	-.03030	.12238	.02738	-.02412	.11344
SHPCORLB	.06400	.21135	.12385	-.06440	.10002	-.01764	.05602	.05260	.07521	.05663	.00945	-.12573
PAPLENDF	.12691	.11031	.09606	.10844	-.15601	.13201	-.07579	-.08754	.31075	.13420	.00576	.63827
DCLL	.15242	.10691	.09859	-.05024	.09673	.08731	.25097	.13756	.05237	.00269	-.00107	-.01874

CHARACTER	ACHLEN	NODF	POSDF	CORLEN	CORLBWI	STYLENG	LENGSTBR	STYLTEX	LENANTH	SHPANAPP	SHPCORLB	PAPLENDF	DCLL
ACHLEN	1.00000												
NODF	.08403	1.00000											
POSDF	.00934	-.16478	1.00000										
CORLEN	-.02239	.12174	.02937	1.00000									
CORLBWI	-.03265	-.06132	-.05773	.22219	1.00000								
STYLENG	.25860	.13352	.08090	.35087	.08144	1.00000							
LENGSTBR	-.07205	.03889	.06638	.16939	-.08458	.19336	1.00000						
STYLTEX	-.12655	-.01598	.04675	.02413	-.03198	-.04758	.40122	1.00000					
LENANTH	-.06420	.25864	-.07183	.11894	-.00216	.00416	.23798	.40219	1.00000				
SHPANAPP	-.08758	.03933	-.04676	.06639	.15900	.06510	.14967	.14968	.04876	1.00000			
SHPCORLB	-.07827	.05007	.02049	.03090	-.08673	.08036	-.01728	-.08543	-.11210	-.08579	1.00000		
PAPLENDF	.34056	.03224	.06073	.20938	.03888	.35000	.13370	.08648	.07316	-.00899	-.01016	1.00000	
DCLL	.03879	-.00525	.00287	.27627	.18674	.26461	.06052	-.10032	.06963	.05736	.08933	.10188	1.00000

APPENDIX SEVEN: TABLE OF ALLELIC FREQUENCIES FOR 47 POPULATIONS OF *PETASITES*

LOCUS-ALLELE	AB01PA N	AB02PA N	AB03PA N	AB04PA N	AB08PA N	BC10PA N	BC12PA N	YT14PA N
Gdh-1	33	34	34	30	10	19	30	32
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-1	0	31	31	30	0	14	28	30
a	0.0000	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000
6Pgd-2	0	1	31	31	0	14	28	30
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	1.0000	0.0000	0.3900	0.4100	0.4000
c	0.0000	0.0000	1.0000	0.0000	0.0000	0.2100	0.1800	0.2000
d	0.0000	1.0000	0.0000	0.0000	0.0000	0.4000	0.4100	0.4000
G6pdh-1	32	34	34	30	0	14	30	32
a	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000
b	1.0000	1.0000	1.0000	0.0000	0.0000	1.0000	1.0000	1.0000
G6pdh-2	32	34	34	30	0	14	30	32
a	0.0000	0.5000	0.5000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	1.0000	0.0000	1.0000	0.9700	1.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
D	1.0000	0.5000	0.5000	0.0000	0.0000	0.0000	0.3300	0.0000
Acp-1	33	34	34	30	10	15	30	32
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Acp-2	33	34	34	30	10	15	26	28
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Lap-1	32	18	11	19	10	18	29	32
a	0.0000	0.0000	0.0000	0.0500	1.0000	1.0000	1.0000	1.0000
b	1.0000	1.0000	1.0000	0.9500	0.0000	0.0000	0.0000	0.0000
Lap-2	32	18	11	26	10	18	29	32
a	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000	1.0000	1.0000
b	1.0000	0.3000	0.7700	1.0000	1.0000	0.0000	0.0000	0.0000
c	0.0000	0.7000	0.2300	0.0000	0.0000	0.0000	0.0000	0.0000
Adh-1	32	31	31	31	10	18	25	32
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0200
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.8800	0.9600
d	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0200
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.1200	0.0000
Adh-2	32	31	31	31	10	18	29	32
a	0.9700	1.0000	1.0000	1.0000	0.7000	0.0600	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.3000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.3000
d	0.0300	0.0000	0.0000	0.0000	0.3000	0.9400	1.0000	0.4000
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Idh-1	32	34	34	0	10	18	29	34
a	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000	1.0000
Pgi-1	17	0	0	21	0	0	0	0
a	1.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000
Pgi-2	11	16	7	19	0	0	0	0
a	0.0000	0.2500	0.2900	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.3400	0.0000	0.0000	0.0000	0.0000
c	0.4500	0.0900	0.0700	0.0300	0.0000	0.0000	0.0000	0.0000
d	0.0000	0.6600	0.6400	0.2600	0.0000	0.0000	0.0000	0.0000
e	0.5500	0.0000	0.0000	0.2100	0.0000	0.0000	0.0000	0.0000
f	0.0000	0.0000	0.0000	0.1600	0.0000	0.0000	0.0000	0.0000
Skdh-1	33	31	33	29	9	9	23	26
a	0.0000	0.5800	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	1.0000	0.4200	0.0600	0.5200	0.6700	0.6700	0.0000	0.0000
c	0.0000	0.0000	0.9400	0.4800	0.3300	0.3300	1.0000	1.0000
Skdh-2	33	31	33	29	9	9	23	26
a	0.8200	0.1900	0.0300	0.5200	0.6100	0.6700	0.0400	0.0400
b	0.1800	0.8100	0.6100	0.4800	0.3900	0.3300	0.0400	0.0200
c	0.0000	0.0000	0.3600	0.0000	0.0000	0.0000	0.9200	0.9400
Pgm-2	0	0	0	29	0	16	25	25
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1000
b	0.0000	0.0000	0.0000	1.0000	0.0000	0.5000	0.5400	0.6200
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.5000	0.4600	0.2800
Pgm-3	0	0	0	29	0	5	19	8
a	0.0000	0.0000	0.0000	1.0000	0.0000	1.0000	0.7400	0.9400
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2600	0.0600
Mnr-2	34	34	34	0	10	19	30	32
a	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000	1.0000

LOCUS-ALLELE	NW21PA N	NW22PA N	YT23PA N	AB05SA N	AB06SA N	AB07SA N	AB09SA N	BC11SA N
Gdh-1	31	28	27	32	30	14	58	11
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-1	34	28	33	32	30	0	58	14
a	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000
6Pgd-2	34	28	33	32	30	0	58	14
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.5000	0.5000	0.2600	1.0000	0.0000	0.0000	0.0000	0.3600
c	0.0000	0.2100	0.5200	0.0000	0.0000	0.0000	0.0000	0.2800
d	0.5000	0.2900	0.2200	0.0000	1.0000	0.0000	1.0000	0.3600
G6pdh-1	32	27	31	32	30	0	60	15
a	0.0000	0.0000	0.0600	1.0000	0.0000	0.0000	0.0000	0.0000
b	1.0000	1.0000	0.9400	0.0000	1.0000	0.0000	1.0000	1.0000
G6pdh-2	32	27	30	32	30	0	60	15
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.5300	0.9600	0.5300	1.0000	0.0000	0.0000	0.2000	1.0000
c	0.4700	0.0000	0.4700	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.0000	0.0400	0.0000	0.0000	1.0000	0.0000	0.8000	0.0000
Acp-1	34	29	24	32	30	7	60	1
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Acp-2	34	29	24	32	30	7	60	14
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Lap-1	34	29	27	22	30	7	55	18
a	1.0000	1.0000	1.0000	0.0200	0.0000	1.0000	0.9700	1.0000
b	0.0000	0.0000	0.0000	0.9800	1.0000	0.0000	0.0300	0.0000
Lap-2	34	29	27	22	30	7	55	18
a	1.0000	1.0000	1.0000	0.0000	0.0000	0.0000	0.9500	1.0000
b	0.0000	0.0000	0.0000	1.0000	1.0000	1.0000	0.0500	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adh-1	34	27	35	31	30	7	60	18
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0200	0.1600	0.0000	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.9600	0.6300	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.0000	0.0200	0.1600	0.0000	0.0000	0.0000	0.0000	0.0000
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	1.0000	0.0000	0.0500	1.0000	1.0000	1.0000	1.0000	1.0000
Adh-2	34	27	35	31	30	7	60	18
a	0.0000	0.0000	0.0000	1.0000	1.0000	1.0000	1.0000	0.1700
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
d	1.0000	1.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.8300
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Idh-1	34	29	34	0	30	4	60	18
a	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000	1.0000
Pgi-1	0	28	0	25	0	0	0	0
a	0.0000	1.0000	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000
Pgi-2	0	28	0	17	0	0	0	0
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.4600	0.0000	0.5000	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.0400	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
e	0.0000	0.5000	0.0000	0.0900	0.0000	0.0000	0.0000	0.0000
F	0.0000	0.0000	0.0000	0.4100	0.0000	0.0000	0.0000	0.0000
Skdh-1	27	18	30	31	30	5	59	6
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.9300	0.2800	0.8300	0.4200	0.0000	0.0000	0.9500	0.0000
c	0.0700	0.7200	0.1700	0.5800	1.0000	1.0000	0.0500	1.0000
Skdh-2	27	18	30	31	30	5	59	6
a	0.8700	0.3100	0.8600	0.4200	0.0000	0.0000	0.0600	0.3300
b	0.0700	0.6900	0.0700	0.5800	1.0000	1.0000	0.8800	0.6700
c	0.0600	0.0000	0.0700	0.0000	0.0000	0.0000	0.0600	0.0000
Pgm-2	32	22	35	31	0	4	0	16
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.5600	0.6600	0.6600	1.0000	0.0000	0.5000	0.0000	0.5000
c	0.4400	0.3400	0.3400	0.0000	0.0000	0.5000	0.0000	0.5000
Pgm-3	32	28	34	31	0	4	0	0
a	0.6400	0.6000	0.6600	0.9800	0.0000	0.5000	0.0000	0.0000
b	0.3600	0.4000	0.3400	0.0200	0.0000	0.5000	0.0000	0.0000
Mnr-2	34	29	34	13	0	7	60	11
a	1.0000	1.0000	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000

LOCUS-ALLELE	BC13SA N	AK30SA N	AK35SA N	YT15FR N	Y161FR N	Y162FR N	YT17FR N	YT18FR N
Gdh-1	20	35	23	18	29	25	18	29
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-1	17	23	22	20	28	30	19	30
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-2	17	23	22	20	28	30	19	30
a	0.0000	0.0000	0.0000	0.2800	0.0000	0.0000	0.1800	0.0000
b	0.4400	0.3900	0.6400	0.0000	0.0400	0.5000	0.0000	0.3200
c	0.1800	0.1300	0.1400	0.4400	0.9600	0.0000	0.8400	0.3600
d	0.3800	0.4800	0.2200	0.2800	0.0000	0.5000	0.1800	0.3200
G6pdh-1	28	21	12	16	26	27	18	30
a	0.0000	1.0000	0.0000	0.0000	1.0000	1.0000	0.0000	0.0000
b	1.0000	0.0000	1.0000	1.0000	0.0000	0.0000	1.0000	1.0000
G6pdh-2	28	13	12	16	26	27	18	30
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.6400	1.0000	0.0800	0.3800	1.0000	1.0000	0.7200	0.0000
c	0.0000	0.0000	0.9200	0.6200	0.0000	0.0000	0.0000	1.0000
d	0.3600	0.0000	0.0000	0.0000	0.0000	0.0000	0.2800	0.0000
Acp-1	17	35	23	10	29	27	17	28
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Acp-2	17	35	23	18	29	27	18	28
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Lap-1	17	10	25	23	25	27	18	30
a	1.0000	0.0000	1.0000	0.0000	1.0000	0.9600	1.0000	1.0000
b	0.0000	1.0000	0.0000	1.0000	0.0000	0.0400	0.0000	0.0000
Lap-2	17	10	25	23	25	27	18	30
a	1.0000	0.3000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
b	0.0000	0.7000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adh-1	17	24	24	18	28	27	15	29
a	0.0000	0.0000	0.1000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.3000	0.4800	0.0200	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.2000	0.1000	0.9000	0.5000	0.5000	1.0000	0.5300
d	0.0000	0.3000	0.0000	0.0200	0.0000	0.0000	0.0000	0.0000
e	0.0000	0.2000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	1.0000	0.0000	0.3200	0.0600	0.5000	0.5000	0.0000	0.4700
Adh-2	17	11	6	18	0	27	15	29
a	0.0600	0.1000	0.0000	0.0000	0.0000	1.0000	0.0000	1.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0300	0.0000
c	0.0000	0.0000	0.0000	0.0600	0.0000	0.0000	0.0700	0.0000
d	0.9400	0.9000	1.0000	0.7800	0.0000	0.0000	0.8000	0.0000
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0300	0.0000
f	0.0000	0.0000	0.0000	0.1600	0.0000	0.0000	0.0700	0.0000
Idh-1	21	24	26	20	29	27	19	30
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Pgi-1	0	0	0	24	0	0	19	0
a	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	1.0000	0.0000
Pgi-2	0	14	17	24	0	25	19	0
a	0.0000	0.0400	0.1200	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.4300	0.4400	0.5000	0.0000	0.5000	0.5000	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.0000	0.1000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
e	0.0000	0.0400	0.0600	0.5000	0.0000	0.5000	0.5000	0.0000
f	0.0000	0.3900	0.3800	0.0000	0.0000	0.0000	0.0000	0.0000
Skdh-1	14	16	7	16	26	21	15	29
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.2900	0.0000	0.0000	0.6200	0.4700	0.0300
c	1.0000	1.0000	0.7100	1.0000	1.0000	0.3800	0.5300	0.9700
Skdh-2	14	16	7	16	26	21	15	29
a	0.2900	0.5000	0.4300	0.2500	0.0000	0.3300	0.0000	0.0300
b	0.5700	0.1900	0.5700	0.7200	0.9300	0.6700	0.4000	0.9700
c	0.1400	0.3100	0.0000	0.0300	0.0700	0.0000	0.6000	0.0000
Pgm-2	15	22	23	17	27	27	10	30
a	0.0000	0.0000	0.0000	0.0000	0.0900	0.0000	0.0000	0.0000
b	0.5000	0.7300	0.7200	0.9400	0.5200	0.5900	0.9500	0.5500
c	0.5000	0.2700	0.2800	0.0600	0.3900	0.4100	0.0500	0.4500
Pgm-3	13	14	21	18	27	27	19	31
a	0.8800	0.9300	0.7600	0.8300	0.6700	0.5600	0.6100	0.5500
b	0.1200	0.0700	0.2400	0.1700	0.3300	0.4400	0.3900	0.4500
Mnr-2	20	23	23	23	29	27	23	31
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000

LOCUS-ALLELE	YT19FR N	YT20FR N	NW21FR N	NW22FR N	YT23FR N	YT24FR N	YT25FR N	AK26FR N
Gdh-1	13	28	25	19	20	23	35	29
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-1	32	28	28	21	22	23	34	29
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-2	32	28	28	21	22	23	34	29
a	0.5000	0.2300	0.5000	0.0000	0.0000	0.4800	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.2400	0.2300	0.0000	0.4900	0.4300
c	0.0000	0.5400	0.5000	0.5700	0.5400	0.0000	0.0600	0.0700
d	0.5000	0.2300	0.0000	0.1900	0.2300	0.5200	0.4500	0.5000
G6pdh-1	26	28	28	21	21	23	33	28
a	0.0000	1.0000	0.0400	0.0000	0.0000	0.0000	0.0000	0.0000
b	1.0000	0.0000	0.9600	1.0000	1.0000	1.0000	1.0000	1.0000
G6pdh-2	26	28	28	21	21	23	33	28
a	0.0000	0.0000	0.0000	0.0000	0.0700	0.0000	0.1000	0.0000
b	0.1900	1.0000	0.1800	1.0000	0.0600	0.8700	0.2800	0.0400
c	0.0000	0.0000	0.8200	0.0000	0.8000	0.0000	0.5200	0.9600
d	0.8100	0.0000	0.0000	0.0000	0.0700	0.1300	0.1000	0.0000
Acp-1	31	28	28	22	22	20	35	29
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Acp-2	31	28	28	22	22	21	34	29
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Lap-1	31	28	28	22	22	25	36	27
a	1.0000	0.5400	1.0000	1.0000	0.0000	0.6800	0.2900	0.0000
b	0.0000	0.4600	0.0000	0.0000	1.0000	0.3200	0.7100	1.0000
Lap-2	31	28	28	22	22	25	36	27
a	0.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000	1.0000
b	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adh-1	32	28	28	24	27	21	34	28
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.2100	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.2900	0.0100	0.0900
c	1.0000	0.5000	0.0000	1.0000	1.0000	0.1000	0.5800	0.7100
d	0.0000	0.0000	0.0000	0.0000	0.0000	0.3800	0.0100	0.1300
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0200	0.0000	0.0000
f	0.0000	0.5000	1.0000	0.0000	0.0000	0.0000	0.4000	0.0700
Xdh-2	32	0	28	28	27	21	33	28
a	0.6700	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0200	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.3300	0.0000	1.0000	0.9600	1.0000	1.0000	1.0000	1.0000
e	0.0000	0.0000	0.0000	0.0200	0.0000	0.0000	0.0000	0.0000
f	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Idh-1	31	28	28	22	22	21	31	29
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Pgi-1	31	0	0	22	0	20	0	0
a	1.0000	0.0000	0.0000	1.0000	0.0000	1.0000	0.0000	0.0000
Pgi-2	31	28	0	22	0	20	0	0
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.5000	0.5000	0.0000	0.4800	0.0000	0.5000	0.0000	0.0000
c	0.0000	0.0000	0.0000	0.0200	0.0000	0.0000	0.0000	0.0000
d	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
e	0.5000	0.5000	0.0000	0.0200	0.0000	0.4300	0.0000	0.0000
f	0.0000	0.0000	0.0000	0.4800	0.0000	0.0700	0.0000	0.0000
Skdh-1	19	27	22	15	9	22	29	20
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0700	0.0200	0.2700	0.0000	0.0900	0.0000	0.2500
c	1.0000	0.9300	0.9800	0.7300	1.0000	0.9100	1.0000	0.7500
Skdh-2	19	27	22	15	15	22	29	20
a	0.2600	0.0400	0.0000	0.1300	0.0000	0.0900	0.1000	0.2000
b	0.7400	0.9600	0.5500	0.8700	0.5000	0.9100	0.8000	0.8000
c	0.0000	0.0000	0.4500	0.0000	0.5000	0.0000	0.1000	0.0000
Pgm-2	26	26	27	22	21	29	34	29
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0300
b	0.6200	0.5800	0.6900	0.6600	0.6200	0.8100	0.6000	0.6700
c	0.3800	0.4200	0.3100	0.3400	0.3800	0.1900	0.4000	0.3000
Pgm-3	26	28	29	22	21	29	34	29
a	0.6000	0.5700	0.6200	0.5200	0.6000	0.5500	0.6800	0.7000
b	0.4000	0.4300	0.3800	0.4800	0.4000	0.4500	0.3200	0.3000
Mnr-2	31	27	28	22	22	21	34	0
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000

LOCUS-ALLELE	AK27FR	AK28FR	AK29FR	AK31FR	AK32FR	AK33FR	AK34FR	AK36FR
	N	N	N	N	N	N	N	N
Gdh-1	26	27	26	24	31	26	33	34
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-1	30	21	27	33	24	24	33	0
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000
6Pgd-2	30	21	27	33	24	24	33	0
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.4500	0.4800	0.5200	0.4700	0.4800	0.4600	0.4500	0.0000
c	0.0000	0.1000	0.0700	0.0600	0.0000	0.0000	0.2600	0.0000
d	0.5500	0.4200	0.4100	0.4700	0.5200	0.5400	0.2900	0.0000
G6pdh-1	30	28	23	26	29	25	30	31
a	0.0000	1.0000	1.0000	1.0000	0.0000	0.0000	0.0000	0.0000
b	1.0000	0.0000	0.0000	0.0000	1.0000	1.0000	1.0000	1.0000
G6pdh-2	30	28	23	24	29	25	30	31
a	0.0000	0.0000	0.0900	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.3800	0.0000	0.1300	1.0000	0.0000	0.0000	0.0300	1.0000
c	0.6200	0.8000	0.6900	0.0000	1.0000	1.0000	0.0000	0.0000
d	0.0000	1.0000	0.0900	0.0000	0.0000	0.0000	0.9700	0.0000
Acp-1	30	28	26	24	31	26	33	30
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Acp-2	30	28	26	24	30	26	33	30
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Lap-1	30	25	21	17	29	26	30	33
a	0.9200	0.8800	0.0000	0.0000	1.0000	1.0000	1.0000	0.7000
b	0.0800	0.1200	1.0000	1.0000	0.0000	0.0000	0.0000	0.3000
Lap-2	30	25	21	17	29	26	30	33
a	0.9000	0.8800	0.0200	0.3500	1.0000	1.0000	1.0000	0.9400
b	0.1000	0.1200	0.9800	0.5900	0.0000	0.0000	0.0000	0.0600
c	0.0000	0.0000	0.0000	0.0600	0.0000	0.0000	0.0000	0.0000
Adh-1	27	29	27	27	31	23	31	31
a	0.0000	0.1700	0.0200	0.0000	0.0000	0.0200	0.2100	0.0000
b	0.0700	0.3100	0.1500	0.4000	0.0000	0.0000	0.4500	0.0800
c	0.5900	0.0700	0.6000	0.2400	0.9500	0.6500	0.2100	0.7100
d	0.1900	0.3800	0.1700	0.0000	0.0000	0.0000	0.0000	0.0800
e	0.0000	0.0700	0.0000	0.3000	0.0000	0.0200	0.0000	0.0000
f	0.1500	0.0000	0.0600	0.0600	0.0500	0.3100	0.1300	0.1300
Adh-2	19	29	27	28	31	23	24	27
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0400	0.0700
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0300	0.0000	0.0000	0.0000
d	0.9500	1.0000	1.0000	1.0000	0.9400	1.0000	0.9600	0.9300
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	0.0500	0.0000	0.0000	0.0000	0.0300	0.0000	0.0000	0.0000
Idh-1	30	28	24	29	31	26	31	31
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Pgi-1	0	21	0	0	25	25	0	0
a	0.0000	1.0000	0.0000	0.0000	1.0000	1.0000	0.0000	0.0000
Pgi-2	0	21	0	23	29	28	22	0
a	0.0000	0.0000	0.0000	0.0400	0.0000	0.0000	0.0200	0.0000
b	0.0000	0.4700	0.0000	0.4800	0.5000	0.5000	0.4800	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.0000	0.0500	0.0000	0.0400	0.0000	0.0000	0.0200	0.0000
e	0.0000	0.4300	0.0000	0.0400	0.4700	0.4500	0.1600	0.0000
f	0.0000	0.0500	0.0000	0.4000	0.0300	0.0500	0.3200	0.0000
Skdh-1	23	24	19	22	29	23	24	25
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.6500	0.2000	0.1000	0.1000	0.0000	0.1700	0.4200	0.1600
c	0.3500	0.8000	0.9000	0.9000	1.0000	0.8300	0.5800	0.8400
Skdh-2	23	24	19	22	29	23	24	25
a	0.4800	0.3000	0.1000	0.5500	0.1000	0.2600	0.2500	0.2400
b	0.5200	0.7000	0.9000	0.2700	0.9000	0.7400	0.7500	0.7400
c	0.0000	0.0000	0.0000	0.1800	0.0000	0.0000	0.0000	0.0200
Pgm-2	30	29	27	35	18	22	30	30
a	0.0000	0.0200	0.0000	0.0200	0.0000	0.0000	0.0000	0.0200
b	0.6200	0.1000	0.6000	0.7700	1.0000	0.5500	0.6800	0.5800
c	0.3800	0.8800	0.4000	0.2100	0.0000	0.4500	0.3200	0.4000
Pgm-3	30	29	27	38	28	26	30	23
a	0.4300	0.6000	0.5700	0.5900	0.5700	0.6700	0.6000	0.6500
b	0.5700	0.4000	0.4300	0.4100	0.4300	0.3300	0.4000	0.3500
Mnr-2	0	28	27	35	31	26	33	34
a	0.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000

LOCUS-ALLELE	AK37FR N	AB38PV N	AB39PV N	AB40PV N	AB41PV N	AB42PV N	AB43PV N
Gdh-1	26	35	35	36	36	36	36
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-1	0	35	35	36	36	36	36
a	0.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
6Pgd-2	0	35	35	36	36	36	36
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
G6pdh-1	28	35	35	36	36	34	36
a	0.0000	0.0000	0.0000	0.0600	0.9200	0.9400	0.0800
b	1.0000	1.0000	1.0000	0.9400	0.0800	0.0600	0.9200
G6pdh-2	28	35	35	36	24	33	36
a	0.0000	0.0000	0.0000	0.0800	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
c	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
d	0.0000	1.0000	1.0000	0.9200	1.0000	1.0000	1.0000
Acp-1	28	35	35	36	36	36	34
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Acp-2	28	35	35	34	36	36	36
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Lap-1	30	26	23	36	36	36	36
a	0.6500	0.1200	0.0900	0.9200	1.0000	1.0000	0.2200
b	0.3500	0.8800	0.9100	0.0800	0.0000	0.0000	0.7800
Lap-2	30	30	29	35	36	36	36
a	0.9000	0.1000	0.0700	1.0000	1.0000	1.0000	0.8200
b	0.1000	0.7800	0.7400	0.0000	0.0000	0.0000	0.1800
c	0.0000	0.1200	0.1900	0.0000	0.0000	0.0000	0.0000
Adh-1	27	30	29	36	36	36	36
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
c	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
d	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Adh-2	28	30	29	36	36	36	36
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
c	0.0000	0.0500	0.0300	0.2500	0.0000	0.0000	0.2500
d	1.0000	0.9000	0.9400	0.5000	1.0000	1.0000	0.5000
e	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
f	0.0000	0.0500	0.0300	0.2500	0.0000	0.0000	0.2500
Idh-1	26	35	35	36	36	36	36
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Pgi-1	0	20	21	36	36	36	36
a	0.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Pgi-2	0	20	21	36	36	36	36
a	0.0000	0.0000	0.0000	0.0400	0.0000	0.0000	0.0800
b	0.0000	0.4500	0.3600	0.4600	0.5000	0.5000	0.4600
c	0.0000	0.0500	0.1400	0.0300	0.0000	0.0000	0.0000
d	0.0000	0.0000	0.0000	0.0100	0.0000	0.0000	0.0000
e	0.0000	0.4800	0.5000	0.0000	0.5000	0.5000	0.0000
f	0.0000	0.0200	0.0000	0.4600	0.0000	0.0000	0.4600
Skdh-1	22	31	28	33	25	28	31
a	0.0000	0.0000	0.0000	0.1200	0.0400	0.1000	0.0300
b	0.7300	0.2300	0.3200	0.8000	0.2000	0.8000	0.3200
c	0.2700	0.7700	0.6800	0.0800	0.7600	0.1000	0.6500
Skdh-2	22	31	31	33	27	23	31
a	0.5200	0.0200	0.0000	0.1500	0.0000	0.0000	0.6500
b	0.4800	0.7900	0.7400	0.8000	0.7000	0.2600	0.2200
c	0.0000	0.1900	0.2600	0.0500	0.3000	0.7400	0.1300
Pgm-2	28	29	35	36	36	32	36
a	0.0500	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
b	0.7400	0.8600	0.6100	0.5100	0.5300	0.7500	0.5600
c	0.2100	0.1400	0.3900	0.4900	0.4700	0.2500	0.4400
Pgm-3	18	32	28	36	36	34	36
a	0.7800	0.7500	0.9500	0.3600	0.6900	0.7600	0.1100
b	0.2200	0.2500	0.0500	0.6400	0.3100	0.2400	0.8900
Mnr-2	28	35	35	36	36	36	36
a	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000

APPENDIX EIGHT: MATRIX OF GENETIC IDENTITIES (ABOVE) AND GENETIC DISTANCES (BELOW) FOR 47 POPULATIONS OF *PETASITES*

	AB01PA	AB02PA	AB03PA	AB04PA	AB08PA	BC10PA	BC12PA	YT14PA	NW21PA	NW22PA	YT23PA	AB05SA	AB06SA	AB07SA	AB09SA	BC11SA
AB01PA		0.8484	0.8353	0.7822	0.8840	0.6807	0.5150	0.4884	0.7017	0.5822	0.6338	0.7743	0.8588	0.7533	0.8056	0.6098
AB02PA	0.1644		0.8604	0.6815	0.7974	0.6887	0.5671	0.5554	0.6784	0.5843	0.6006	0.6898	0.8865	0.7827	0.8431	0.6820
AB03PA	0.1799	0.1504		0.7208	0.8245	0.6603	0.6364	0.6294	0.6057	0.6018	0.5977	0.7356	0.8934	0.8882	0.7316	0.7254
AB04PA	0.2456	0.3835	0.3274		0.8741	0.6770	0.5442	0.5635	0.6251	0.6228	0.5688	0.9955	0.7168	0.8114	0.6059	0.6470
AB08PA	0.1233	0.2264	0.1929	0.1345		0.8622	0.6726	0.6577	0.8425	0.7313	0.7713	0.8746	0.8008	0.9174	0.8712	0.8242
BC10PA	0.3847	0.3730	0.4151	0.3900	0.1483		0.8697	0.8441	0.9696	0.9062	0.9217	0.6903	0.6193	0.7490	0.8419	0.9649
BC12PA	0.6637	0.5672	0.4519	0.6085	0.3966	0.1396		0.9760	0.8247	0.9461	0.8781	0.5789	0.5847	0.6920	0.7117	0.8970
YT14PA	0.7167	0.5881	0.4630	0.5735	0.4190	0.1695	0.0243		0.7863	0.9223	0.8542	0.5966	0.5613	0.6832	0.6970	0.8690
NW21PA	0.3543	0.3880	0.5014	0.4699	0.1713	0.0309	0.1928	0.2404		0.8660	0.9400	0.6363	0.5749	0.6923	0.8291	0.8973
NW22PA	0.5409	0.5373	0.5077	0.4735	0.3130	0.0985	0.0554	0.0809	0.1438		0.9320	0.6467	0.5885	0.7325	0.7523	0.9254
YT23PA	0.4561	0.5098	0.5147	0.5643	0.2597	0.0815	0.1300	0.1576	0.0619	0.0704		0.5859	0.5049	0.6386	0.7570	0.8576
AB05SA	0.2558	0.3714	0.3071	0.0045	0.1340	0.3706	0.5466	0.5166	0.4521	0.4359	0.5346		0.7327	0.8427	0.6313	0.6789
AB06SA	0.1523	0.1205	0.1127	0.3330	0.2222	0.4792	0.5366	0.5775	0.5536	0.5302	0.6834	0.3110		0.9000	0.7950	0.6943
AB07SA	0.2833	0.2450	0.1185	0.2090	0.0863	0.2890	0.3682	0.3809	0.3677	0.3113	0.4485	0.1711	0.1054		0.8316	0.8442
AB09SA	0.2161	0.1707	0.3125	0.5010	0.1379	0.1721	0.3401	0.3610	0.1874	0.2847	0.2784	0.4599	0.2294	0.1844		0.8154
BC11SA	0.4947	0.3828	0.3210	0.4355	0.1934	0.0357	0.1087	0.1404	0.1084	0.0776	0.1536	0.3873	0.3648	0.1694	0.2041	
BC13SA	0.4510	0.3689	0.3115	0.4387	0.2097	0.0433	0.0897	0.1321	0.0993	0.0873	0.1478	0.3934	0.3316	0.1951	0.1864	0.0062
AK30SA	0.5131	0.4869	0.3883	0.1861	0.3180	0.2908	0.2502	0.2671	0.3678	0.2664	0.3078	0.1609	0.3981	0.3310	0.5833	0.2783
AK35SA	0.5465	0.4849	0.4565	0.5240	0.2295	0.1068	0.1506	0.1832	0.0884	0.1068	0.0780	0.4642	0.4918	0.2643	0.2633	0.1024
YT15FR	0.4441	0.4117	0.3213	0.4355	0.4804	0.2439	0.1759	0.1805	0.2832	0.1154	0.1806	0.3902	0.3519	0.4103	0.3957	0.1989
Y161FR	0.7100	0.5645	0.3597	0.3668	0.2452	0.2030	0.1844	0.1919	0.3127	0.1386	0.2298	0.3202	0.5309	0.1207	0.3330	0.1298
Y162FR	0.4746	0.4233	0.4953	0.2329	0.1549	0.1833	0.2527	0.2437	0.2222	0.1733	0.2231	0.2220	0.4700	0.1589	0.1833	0.1848
YT17FR	0.5002	0.5394	0.4358	0.5462	0.3330	0.1501	0.0530	0.0656	0.1885	0.0410	0.0793	0.5033	0.5480	0.3665	0.2615	0.1457
YT18FR	0.4891	0.3396	0.2744	0.5187	0.2321	0.2397	0.2266	0.2204	0.2460	0.1721	0.2183	0.4564	0.3150	0.1091	0.1508	0.1535
YT19FR	0.3074	0.3697	0.3047	0.4343	0.1675	0.3187	0.2090	0.2307	0.3648	0.1610	0.2794	0.3937	0.2036	0.1010	0.2618	0.2515
YT20FR	0.5874	0.4614	0.3565	0.2792	0.2702	0.2049	0.1962	0.2089	0.2983	0.1331	0.2422	0.2448	0.3993	0.1431	0.3011	0.1337
NW21FR	0.5527	0.4660	0.3147	0.5930	0.2429	0.1371	0.1487	0.1911	0.1467	0.1573	0.1637	0.5255	0.4461	0.2048	0.2797	0.0828
NW22FR	0.6078	0.5507	0.4667	0.5211	0.3311	0.1249	0.0724	0.0965	0.1845	0.0194	0.0868	0.4562	0.5368	0.2975	0.2954	0.0855
YT23FR	0.5435	0.4300	0.2971	0.6085	0.5429	0.2966	0.1486	0.1793	0.2995	0.1514	0.1909	0.5314	0.4081	0.4431	0.4541	0.2392
YT24FR	0.5090	0.4363	0.4320	0.4784	0.3455	0.1398	0.1208	0.1556	0.1959	0.0617	0.1549	0.4258	0.3776	0.2801	0.2620	0.0842
YT25FR	0.3352	0.2913	0.2131	0.3374	0.2272	0.2408	0.1977	0.2396	0.2642	0.1639	0.2470	0.2929	0.1941	0.1758	0.3818	0.1862
AK26FR	0.5182	0.3785	0.3895	0.5100	0.5109	0.2590	0.2236	0.2580	0.2399	0.1563	0.1832	0.4949	0.3583	0.4517	0.3938	0.2384
AK27FR	0.4826	0.4248	0.5156	0.5340	0.2424	0.1028	0.1301	0.1720	0.0665	0.0521	0.0378	0.5422	0.4713	0.3404	0.2227	0.1214
AK28FR	0.4966	0.5317	0.5110	0.4827	0.2655	0.2600	0.2376	0.3230	0.2802	0.1931	0.2469	0.4394	0.4407	0.2672	0.3083	0.2334
AK29FR	0.4739	0.4148	0.3426	0.2752	0.3188	0.4302	0.3648	0.4156	0.4320	0.2999	0.3652	0.2370	0.3246	0.2564	0.5778	0.3754
AK31FR	0.5136	0.4863	0.4263	0.2046	0.3166	0.2849	0.2556	0.2912	0.3303	0.2411	0.2847	0.1754	0.4214	0.3377	0.5652	0.2675
AK32FR	0.6202	0.5309	0.5122	0.5872	0.3543	0.2268	0.1438	0.1644	0.2092	0.0754	0.1429	0.5267	0.4691	0.2916	0.3139	0.1658
AK33FR	0.5244	0.4730	0.4822	0.5556	0.2652	0.1430	0.1278	0.1631	0.1228	0.0708	0.1008	0.5030	0.4445	0.2456	0.2569	0.1146
AK34FR	0.4322	0.4173	0.4056	0.5909	0.2506	0.1369	0.1378	0.1989	0.1469	0.0967	0.1135	0.5227	0.3758	0.2676	0.1729	0.1275
AK36FR	0.5187	0.4389	0.3726	0.4854	0.2872	0.1004	0.0652	0.0928	0.1648	0.0091	0.0954	0.4238	0.4367	0.2540	0.2780	0.0667
AK37FR	0.4429	0.4584	0.4692	0.6307	0.2880	0.1862	0.1953	0.2208	0.1343	0.1100	0.0532	0.5733	0.5907	0.4088	0.3107	0.2512
AB38PV	0.2659	0.2817	0.3034	0.4512	0.3254	0.3549	0.2353	0.2815	0.3814	0.1981	0.3082	0.4068	0.1654	0.2951	0.3221	0.3338
AB39PV	0.2520	0.2719	0.3062	0.4626	0.3311	0.3376	0.2327	0.2799	0.3746	0.2096	0.3072	0.4218	0.1767	0.3199	0.3220	0.3390
AB40PV	0.3930	0.3545	0.5254	0.6928	0.3065	0.2322	0.1993	0.2380	0.2072	0.1406	0.1569	0.6176	0.3960	0.3608	0.1346	0.2518
AB41PV	0.5836	0.5375	0.5968	0.5855	0.3507	0.2851	0.1618	0.2185	0.3066	0.1484	0.2325	0.5316	0.4586	0.3111	0.2809	0.2607
AB42PV	0.5248	0.5523	0.6961	0.5844	0.3526	0.2870	0.1806	0.2399	0.2688	0.1972	0.2028	0.5496	0.6034	0.4620	0.2703	0.3615
AB43PV	0.2847	0.3173	0.3818	0.5931	0.3469	0.3213	0.2136	0.2628	0.2783	0.1950	0.2170	0.5243	0.2663	0.4049	0.2581	0.2785

	BC13SA	AK30SA	AK35SA	YT15FR	Y161FR	Y162FR	YT17FR	YT18FR	YT19FR	YT20FR	NW21FR	NW22FR	YT23FR	YT24FR	YT25FR	AK26FR
AB01PA	0.6370	0.5986	0.5790	0.6414	0.4916	0.6221	0.6064	0.6132	0.7354	0.5558	0.5754	0.5445	0.5807	0.6011	0.7152	0.5956
AB02PA	0.6915	0.6145	0.6157	0.6625	0.5686	0.6549	0.5831	0.7121	0.6909	0.6304	0.6275	0.5765	0.6505	0.6465	0.7473	0.6849
AB03PA	0.7323	0.6782	0.6335	0.7252	0.6079	0.6094	0.6467	0.7600	0.7373	0.7001	0.7300	0.6271	0.7430	0.6492	0.8080	0.6774
AB04PA	0.6449	0.8302	0.5922	0.6469	0.6930	0.7922	0.5791	0.5953	0.6477	0.7564	0.5527	0.5939	0.5442	0.6198	0.7136	0.6005
AB08PA	0.8108	0.7276	0.7950	0.6185	0.7825	0.8565	0.7168	0.7929	0.8458	0.7632	0.7843	0.7181	0.5811	0.7079	0.7968	0.6000
BC10PA	0.9577	0.7477	0.8987	0.7835	0.8162	0.8326	0.8606	0.7869	0.7271	0.8147	0.8719	0.8826	0.7434	0.8696	0.7860	0.7718
BC12PA	0.9142	0.7787	0.8602	0.8387	0.8316	0.7767	0.9483	0.7972	0.8114	0.8218	0.8618	0.9302	0.8619	0.8862	0.8206	0.7996
YT14PA	0.8762	0.7656	0.8326	0.8349	0.8254	0.7837	0.9365	0.8022	0.7940	0.8115	0.8261	0.9080	0.8359	0.8559	0.7870	0.7726
NW21PA	0.9055	0.6922	0.9154	0.7533	0.7315	0.8007	0.8282	0.7819	0.6944	0.7421	0.8636	0.8315	0.7412	0.8221	0.7678	0.7867
NW22PA	0.9164	0.7661	0.8987	0.8910	0.8706	0.8409	0.9599	0.8419	0.8513	0.8754	0.8544	0.9808	0.8595	0.9402	0.8488	0.8553
YT23PA	0.8626	0.7351	0.9250	0.8348	0.7947	0.8001	0.9238	0.8039	0.7563	0.7849	0.8490	0.9169	0.8262	0.8565	0.7811	0.8326
AB05SA	0.6748	0.8514	0.6287	0.6769	0.7260	0.8009	0.6045	0.6336	0.6746	0.7829	0.5913	0.6337	0.5878	0.6533	0.7461	0.6097
AB06SA	0.7177	0.6716	0.6115	0.7033	0.5881	0.6250	0.5781	0.7298	0.8158	0.6708	0.6401	0.5846	0.6649	0.6855	0.8236	0.6989
AB07SA	0.8227	0.7182	0.7678	0.6634	0.8863	0.8531	0.6931	0.8966	0.9039	0.8667	0.8148	0.7427	0.6420	0.7557	0.8387	0.6365
AB09SA	0.8299	0.5581	0.7685	0.6732	0.7168	0.8325	0.7698	0.8346	0.7696	0.7400	0.7560	0.7442	0.6350	0.7695	0.6826	0.6745
BC11SA	0.9938	0.7571	0.9026	0.8197	0.8782	0.8313	0.8644	0.8577	0.7777	0.8749	0.9206	0.9181	0.7872	0.9193	0.8301	0.7879
BC13SA		0.7640	0.9221	0.8282	0.8602	0.8078	0.8712	0.8533	0.8005	0.8540	0.9319	0.8989	0.8091	0.9107	0.8479	0.8110
AK30SA	0.2692		0.7414	0.8088	0.7983	0.7672	0.7270	0.6362	0.7132	0.8525	0.6956	0.7557	0.7846	0.8026	0.8433	0.7750
AK35SA	0.0811	0.2992		0.8551	0.7940	0.7650	0.8565	0.8031	0.7671	0.7829	0.9308	0.8877	0.8594	0.8885	0.8549	0.8972
YT15FR	0.1885	0.2122	0.1565		0.7895	0.7215	0.8888	0.8324	0.8039	0.8538	0.8505	0.8802	0.9694	0.9061	0.8869	0.9631
Y161FR	0.1505	0.2253	0.2307	0.2363		0.9172	0.8546	0.8383	0.7401	0.9762	0.8420	0.8972	0.7627	0.8376	0.7403	0.7094
Y162FR	0.2134	0.2650	0.2679	0.3264	0.0865		0.8008	0.8265	0.7549	0.9387	0.7326	0.8121	0.6721	0.7922	0.6919	0.6874
YT17FR	0.1379	0.3189	0.1549	0.1179	0.1571	0.2222		0.8196	0.8441	0.8472	0.8713	0.9549	0.8673	0.9098	0.7992	0.8124
YT18FR	0.1586	0.4522	0.1130	0.1835	0.1764	0.1905	0.1989		0.8314	0.8312	0.8824	0.8471	0.8313	0.8184	0.8070	0.8334
YT19FR	0.2226	0.3379	0.2651	0.2182	0.3010	0.2812	0.1694	0.1846		0.7616	0.7604	0.8309	0.7565	0.8356	0.8757	0.7330
YT20FR	0.1579	0.1596	0.2448	0.1581	0.0241	0.0633	0.1658	0.1848	0.2724		0.8305	0.8754	0.8096	0.8824	0.7869	0.7839
NW21FR	0.0705	0.3629	0.0717	0.1619	0.1719	0.3111	0.1378	0.1251	0.2739	0.1857		0.8616	0.8529	0.8793	0.8293	0.8280
NW22FR	0.1065	0.2802	0.1191	0.1276	0.1084	0.2081	0.0462	0.1659	0.1852	0.1331	0.1490		0.8639	0.9258	0.8362	0.8405
YT23FR	0.2119	0.2426	0.1515	0.0311	0.2709	0.3974	0.1424	0.1847	0.2790	0.2112	0.1591	0.1463		0.8469	0.8889	0.9664
YT24FR	0.0935	0.2199	0.1182	0.0986	0.1772	0.2330	0.0946	0.2005	0.1797	0.1251	0.1286	0.0771	0.1662		0.8508	0.8652
YT25FR	0.1650	0.1704	0.1567	0.1200	0.3007	0.3684	0.2241	0.2144	0.1327	0.2396	0.1872	0.1789	0.1178	0.1616		0.8978
AK26FR	0.2095	0.2549	0.1085	0.0376	0.3433	0.3748	0.2078	0.1823	0.3106	0.2435	0.1888	0.1738	0.0342	0.1448	0.1078	
AK27FR	0.1229	0.3252	0.0477	0.1581	0.2595	0.2135	0.1015	0.1520	0.2232	0.2340	0.1413	0.0769	0.1584	0.1050	0.1603	0.1023
AK28FR	0.1781	0.2320	0.2004	0.2964	0.1780	0.2111	0.2510	0.2987	0.2415	0.1599	0.2659	0.2289	0.3015	0.1810	0.2767	0.2952
AK29FR	0.3468	0.0988	0.2763	0.1946	0.2766	0.3281	0.3732	0.3436	0.2662	0.1884	0.3393	0.3134	0.1848	0.2757	0.0886	0.1679
AK31FR	0.2692	0.0091	0.2775	0.2101	0.2177	0.2469	0.3055	0.4484	0.3473	0.1415	0.3536	0.2530	0.2345	0.2056	0.1690	0.2366
AK32FR	0.1482	0.3587	0.0643	0.0940	0.2390	0.2764	0.1072	0.0961	0.1731	0.2217	0.1166	0.1003	0.1088	0.1102	0.1410	0.0889
AK33FR	0.0935	0.3488	0.0328	0.1103	0.2234	0.2456	0.1196	0.0831	0.1806	0.2077	0.0812	0.1010	0.1114	0.1074	0.1276	0.0800
AK34FR	0.0849	0.3351	0.0687	0.1971	0.2263	0.2587	0.1110	0.1771	0.1790	0.2323	0.1437	0.1043	0.1984	0.0985	0.1993	0.1838
AK36FR	0.0746	0.2160	0.1058	0.0867	0.1089	0.1971	0.0549	0.1763	0.1763	0.1038	0.1285	0.0113	0.1230	0.0286	0.1320	0.1291
AK37FR	0.2164	0.3612	0.0695	0.0979	0.3061	0.3189	0.1125	0.1798	0.2512	0.2925	0.1590	0.1251	0.1024	0.1772	0.1700	0.0696
AB38PV	0.2650	0.2437	0.2910	0.1292	0.4181	0.4197	0.1887	0.3283	0.1058	0.3074	0.3359	0.2263	0.1569	0.1787	0.0861	0.1592
AB39PV	0.2634	0.2464	0.3029	0.1438	0.4321	0.4318	0.2049	0.3469	0.1214	0.3234	0.3499	0.2430	0.1614	0.1998	0.0927	0.1642
AB40PV	0.2206	0.4547	0.2037	0.2368	0.3213	0.2577	0.1319	0.2244	0.1799	0.2932	0.2878	0.1324	0.2435	0.1801	0.2753	0.2262
AB41PV	0.1984	0.2823	0.2364	0.2264	0.1768	0.2003	0.1476	0.2695	0.1802	0.1528	0.2624	0.1772	0.2372	0.1778	0.2710	0.2602
AB42PV	0.2780	0.3306	0.2833	0.2944	0.2722	0.2184	0.1413	0.3752	0.2610	0.2428	0.3258	0.2347	0.3009	0.2504	0.3687	0.3301
AB43PV	0.2650	0.3040	0.2642	0.1718	0.3983	0.3487	0.1936	0.2929	0.1848	0.3058	0.3368	0.1968	0.1615	0.2013	0.2106	0.1763

	AK27FR	AK28FR	AK29FR	AK31FR	AK32FR	AK33FR	AK34FR	AK36FR	AK37FR	AB38PV	AB39PV	AB40PV	AB41PV	AB42PV	AB43PV
AB01PA	0.6172	0.6086	0.6226	0.5983	0.5379	0.5919	0.6491	0.5953	0.6422	0.7665	0.7772	0.6750	0.5579	0.5917	0.7522
AB02PA	0.6539	0.5876	0.6604	0.6149	0.5881	0.6231	0.6588	0.6447	0.6323	0.7545	0.7620	0.7015	0.5842	0.5756	0.7281
AB03PA	0.5971	0.5999	0.7099	0.6529	0.5992	0.6174	0.6666	0.6890	0.6131	0.7383	0.7362	0.5913	0.5506	0.4985	0.6826
AB04PA	0.5863	0.6171	0.7595	0.8149	0.5559	0.5737	0.5538	0.6155	0.5322	0.6369	0.6297	0.5002	0.5568	0.5575	0.5526
AB08PA	0.7847	0.7668	0.7270	0.7286	0.7016	0.7671	0.7784	0.7504	0.7498	0.7222	0.7181	0.7360	0.7042	0.7028	0.7069
BC10PA	0.9023	0.7711	0.6504	0.7521	0.7970	0.8668	0.8721	0.9045	0.8301	0.7013	0.7135	0.7928	0.7520	0.7505	0.7252
BC12PA	0.8780	0.7885	0.6945	0.7744	0.8660	0.8800	0.8712	0.9369	0.8226	0.7903	0.7924	0.8193	0.8506	0.8265	0.8077
YT14PA	0.8420	0.7239	0.6598	0.7474	0.8484	0.8495	0.8196	0.9114	0.8019	0.7546	0.7558	0.7882	0.8037	0.7867	0.7689
NW21PA	0.9357	0.7557	0.6492	0.7187	0.8112	0.8845	0.8634	0.8480	0.8743	0.6829	0.6876	0.8128	0.7360	0.7643	0.7571
NW22PA	0.9492	0.8244	0.7409	0.7857	0.9274	0.9317	0.9078	0.9909	0.8959	0.8203	0.8189	0.8688	0.8621	0.8211	0.8228
YT23PA	0.9629	0.7812	0.6941	0.7522	0.8668	0.9040	0.8927	0.9054	0.9482	0.7348	0.7355	0.8548	0.7925	0.8165	0.8049
AB05SA	0.5815	0.6444	0.7890	0.8391	0.5906	0.6047	0.5929	0.6546	0.5636	0.6658	0.6558	0.5392	0.5876	0.5772	0.5919
AB06SA	0.6242	0.6436	0.7228	0.6561	0.6256	0.6411	0.6867	0.6461	0.5539	0.8475	0.8381	0.6730	0.6322	0.5469	0.7662
AB07SA	0.7115	0.7656	0.7738	0.7134	0.7471	0.7822	0.7652	0.7757	0.6644	0.7444	0.7262	0.6971	0.7327	0.6300	0.6670
AB09SA	0.8004	0.7347	0.5611	0.5683	0.7306	0.7735	0.8412	0.7573	0.7330	0.7246	0.7247	0.8741	0.7551	0.7631	0.7725
BC11SA	0.8857	0.7919	0.6870	0.7653	0.8472	0.8918	0.8803	0.9411	0.7779	0.7162	0.7125	0.7774	0.7705	0.6966	0.7569
BC13SA	0.8844	0.8368	0.7070	0.7640	0.8622	0.9107	0.9186	0.9282	0.8054	0.7672	0.7684	0.8020	0.8200	0.7573	0.7672
AK30SA	0.7224	0.7929	0.9059	0.9809	0.6985	0.7112	0.7153	0.8058	0.6968	0.7837	0.7816	0.6346	0.7540	0.7185	0.7378
AK35SA	0.9534	0.8184	0.7586	0.7577	0.9377	0.9678	0.9336	0.8996	0.9329	0.7475	0.7387	0.8157	0.7895	0.7533	0.7678
YT15FR	0.8538	0.7435	0.8232	0.8105	0.9103	0.8956	0.8211	0.9170	0.9067	0.8788	0.8661	0.7891	0.7974	0.7450	0.8421
Y161FR	0.7714	0.8370	0.7584	0.8044	0.7874	0.7998	0.7975	0.8969	0.7363	0.6583	0.6491	0.7252	0.8380	0.7617	0.6715
Y162FR	0.8077	0.8097	0.7203	0.7812	0.7585	0.7822	0.7721	0.8211	0.7269	0.6573	0.6493	0.7728	0.8185	0.8038	0.7056
YT17FR	0.9035	0.7781	0.6885	0.7367	0.8983	0.8873	0.8949	0.9465	0.8936	0.8280	0.8147	0.8765	0.8627	0.8682	0.8240
YT18FR	0.8590	0.7418	0.7092	0.6387	0.9084	0.9203	0.8377	0.8384	0.8354	0.7201	0.7069	0.7990	0.7638	0.6872	0.7461
YT19FR	0.8000	0.7855	0.7663	0.7066	0.8410	0.8348	0.8361	0.8384	0.7778	0.8996	0.8857	0.8354	0.8351	0.7703	0.8313
YT20FR	0.7913	0.8522	0.8283	0.8580	0.8012	0.8124	0.7927	0.9014	0.7464	0.7354	0.7237	0.7459	0.8583	0.7844	0.7366
NW21FR	0.8682	0.7665	0.7123	0.7022	0.8900	0.9220	0.8661	0.8794	0.8530	0.7147	0.7047	0.7499	0.7692	0.7220	0.7141
NW22FR	0.9260	0.7954	0.7310	0.7765	0.9045	0.9039	0.9010	0.9888	0.8824	0.7975	0.7843	0.8760	0.8376	0.7908	0.8214
YT23FR	0.8535	0.7397	0.8313	0.7910	0.8959	0.8946	0.8200	0.8843	0.9027	0.8548	0.8509	0.7839	0.7888	0.7401	0.8509
YT24FR	0.9003	0.8344	0.7590	0.8142	0.8957	0.8982	0.9062	0.9719	0.8376	0.8364	0.8189	0.8352	0.8371	0.7785	0.8177
YT25FR	0.8519	0.7583	0.9152	0.8445	0.8685	0.8802	0.8193	0.8763	0.8437	0.9175	0.9114	0.7594	0.7626	0.6917	0.8101
AK26FR	0.9027	0.7444	0.8454	0.7893	0.9149	0.9231	0.8321	0.8789	0.9327	0.8529	0.8486	0.7975	0.7709	0.7188	0.8383
AK27FR		0.8029	0.7532	0.7538	0.9342	0.9639	0.9140	0.9326	0.9623	0.7917	0.7830	0.8998	0.8239	0.8117	0.8437
AK28FR	0.2195		0.8124	0.7993	0.7912	0.8374	0.8915	0.7941	0.7313	0.7743	0.7812	0.8221	0.9306	0.8690	0.7969
AK29FR	0.2834	0.2078		0.9127	0.7811	0.7824	0.7211	0.7601	0.7644	0.8456	0.8382	0.6822	0.7864	0.7203	0.7545
AK31FR	0.2827	0.2241	0.0913		0.7184	0.7266	0.7382	0.8203	0.7153	0.7838	0.7714	0.6662	0.7620	0.7267	0.7714
AK32FR	0.0681	0.2342	0.2470	0.3308		0.9825	0.8842	0.9016	0.9329	0.8314	0.8074	0.8469	0.8573	0.7999	0.8098
AK33FR	0.0368	0.1775	0.2454	0.3194	0.0176		0.9057	0.9143	0.9502	0.8183	0.8123	0.8623	0.8643	0.8110	0.8170
AK34FR	0.0908	0.1149	0.3269	0.3036	0.1231	0.0990		0.8954	0.8633	0.8303	0.8196	0.9114	0.8740	0.8398	0.8517
AK36FR	0.0648	0.2306	0.2743	0.1980	0.1036	0.0896	0.1105		0.8826	0.8327	0.8256	0.8571	0.8392	0.7723	0.8366
AK37FR	0.0384	0.3129	0.2686	0.3351	0.0654	0.0511	0.1470	0.1249		0.8234	0.8226	0.8760	0.8084	0.8135	0.8344
AB38PV	0.2335	0.2558	0.1677	0.2436	0.1847	0.2005	0.1859	0.1831	0.1943		0.9952	0.8533	0.8524	0.8171	0.8978
AB39PV	0.2446	0.2469	0.1766	0.2596	0.2140	0.2079	0.1989	0.1916	0.1953	0.0049		0.8454	0.8501	0.8198	0.8809
AB40PV	0.1059	0.1959	0.3824	0.4061	0.1662	0.1481	0.0928	0.1542	0.1323	0.1587	0.1668		0.8950	0.8914	0.9276
AB41PV	0.1937	0.0720	0.2403	0.2718	0.1539	0.1458	0.1346	0.1753	0.2127	0.1597	0.1624	0.1110		0.9636	0.8492
AB42PV	0.2086	0.1405	0.3281	0.3192	0.2233	0.2095	0.1746	0.2584	0.2065	0.2020	0.1987	0.1150	0.0371		0.8218
AB43PV	0.1700	0.2270	0.2817	0.2596	0.2110	0.2021	0.1605	0.1784	0.1811	0.1078	0.1268	0.0751	0.1634	0.1963	